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PLANKTON OF THE FLORIDA CURRENT. PART VI. THE CHAETOGNATHA [1]

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ABSTRACT

Plankton collections from 0-350 meters at a station located 10 miles east of Miami, taken during the period from June 19, 1950, to February 4, 1952, provided material for studies of relative abundance of species, seasonal variation in abundance and vertical distribution, and breeding periods. Data on diurnal migration was obtained during a 24-hour period by sampling 0-731 meters at a station 40 miles east of Miami.

In order of relative abundance, species at the 10-mile station were: *Sagitta enflata, S. serratodentata, S. minima, Pterosagitta draco, S. bipunctata, Krohnitta pacifica, S. decipiens, S. hispida, S. hexaptera, S. lyra* and *K. subtilis, S. helenae,* and, each forming less than 0.1 per cent of the total, *S. planctonis, S. macrocephala* and *Eukrohnia hamata.* With the exception of *S. helenae* and *E. hamata* and the addition of *E. fowleri,* these species also were collected at the 40-mile station.

Species collected in adequate numbers showed seasonal maxima in abundance which usually occurred in summer and sometimes also in another season. The maxima of some coincided generally with their major breeding periods.

Differences in relative abundance suggest the presence at the 10-mile station of neritic influence which is lacking at the 40-mile station.

No correlation was found between periods of abundance of any species and percentage of either the Gulf of Mexico or Yucatan components of the Florida Current at the 10-mile station. However, it is suggested that *S. hispida* may be an indicator of Gulf water under certain conditions.

Vertical distribution was highly variable seasonally. The depths at which the major concentrations of each species live were much greater at the 40-mile than at the 10-mile station. It is believed that this results principally from reaction to temperature.

Sagitta enflata, S. hexaptera, S. lyra, S. serratodentata and *Pterosagitta draco* were found to migrate diurnally. There is also evidence of diurnal migration by *S. decipiens, K. subtilis* and *K. pacifica.*

From a study of length and maturity stages, it is concluded that length is not a generally useful index of stage of maturity and that several species may spawn more than once in a lifespan. Data on length at each stage of maturity of species collected in both the Florida Current off Miami and in colder waters indicate that the animals may mature at a smaller size in

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tropical oceanic waters. Evidence is given that six Florida Current species breed more or less continually throughout the year in addition to their major breeding periods and that two breed only at certain seasons. There were insufficient data to determine the spawning periods of remaining species.

Introduction

The National Geographic Society, in cooperation with The Marine Laboratory of the University of Miami, initiated in June, 1950, an investigation of the plankton and hydrography of the Florida Current which was terminated in February, 1952. All observations and collections were made at one location (25° 43′ - 26° 08′ N, 79° 56′ W), somewhat east of the axis of the Current and hereinafter referred to as the NG station. The depth is approximately 350 meters. The hydrographic equipment, plankton nets and the depth-distance recorder used have been described by Miller *et al.* (1953). The plankton collections and hydrographic data obtained at the NG station were the major materials used by the writer in a study of relative abundance, seasonal variations in abundance, vertical distribution and breeding periods of the Chaetognatha.

Additional sources of material were: samples collected on a 24-hour station, which was part of an investigation of the scattering layer[1] and is hereinafter referred to as the SL station (SL 18), occupied July 1, 1953, on the eastern side of the Current, about 40 miles from Miami; and two series of hauls (*Culver* station 214, May 28, 1940; *Culver* station 221, July 31, 1940) taken off Bermuda by H. B. Moore.

In identifying and counting chaetognaths, all specimens in samples of five cc. or less total volume (wet, drained) were examined; larger catches were subsampled and then the entire sample was examined for uncommon species. Depending on the volume of the sample, the subsample was 0.1 to 0.5 of the total. The specimens in each sample or subsample were put into vials according to species for subsequent measurement and examination of gonads.

Treatment of the data on vertical distribution has been patterned after the work of Moore (1949) in Bermuda waters, and these data, together with those on seasonal variations in abundance, have been compared with Moore's findings.

Tabular summaries of numbers of each species per sample, of numbers per 10 cc. of plankton, and all other data on which this

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study is based are on file at The Marine Laboratory of the University of Miami.

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Relative Abundance and Seasonal Variation in Abundance

Sixteen species of Chaetognatha occur in the Florida Current off Miami. These are *Sagitta enflata* Grassi, *S. hexaptera* d'Orbigny, *S. lyra* Krohn, *S. bipunctata* Quoy and Gaimard, *S. hispida* Conant, *S. helenae* Ritter-Záhony, *S. serratodentata* Krohn, *S. minima* Grassi, *S. decipiens* Fowler, *S. planctonis* Steinhaus, *S. macrocephala* Fowler, *Pterosagitta draco* (Krohn), *Krohnitta subtilis* (Grassi), *K. pacifica* (Aida), *Eukrohnia hamata* (Möbius) and *E. fowleri* Ritter-Záhony. Specimens of these, except *S. serratodentata, S. planctonis, S. macrocephala, Pterosagitta draco, Eukrohnia hamata* and *E. fowleri,* were sent to J. H. Fraser, who confirmed the identifications.

All of the above except *Eukrohnia fowleri* were taken at the NG station. At the SL station, *Sagitta helenae* and *E. hamata* were lacking. Seasonal variation in abundance of the commoner species at the NG station during the period from June 19, 1950, to February 4, 1952, is shown in Figures 1-4. Since estimated numbers of each species per mile are not known for many samples because of the failure of the depth-distance recorder, and since the wet volume of drained plankton is known for each sample, the figures used are numbers per 10 cc. of plankton. This measure is deemed adequate to show relative abundance and seasonal variation in abundance in view of the absence of marked seasonal fluctuation in quantity of zooplankton (Miller *et al.*, 1953).

The two most abundant species at both stations are *S. enflata* and *S. serratodentata,* the former being the dominant species on the western side of the Current, and the latter replacing it on the eastern side (Table 1).

Individual Species

Sagitta enflata.—Long known to be a widely distributed species in tropical and subtropical oceans (Ritter-Záhony, 1911a; Germain and Joubin, 1916; Michael, 1919; Bollmann, 1932; Thomson, 1947;

TABLE 1

TOTAL COUNTS AND PERCENTAGES AT THE NG STATION AND AT SL 18.

SPECIES	NG TOTAL NUMBERS	% OF TOTAL	SL 18 TOTAL NUMBERS	% OF TOTAL
Sagitta enflata	34,398	54.5	467	14.7
S. hexaptera	484	0.8	145	4.5
S. lyra	427	0.7	67	2.1
S. bipunctata	2,980	4.7	52	1.6
S. hispida	857	1.4	12	0.4
S. helenae	318	0.5	0	0.0
S. serratodentata	12,598	19.9	1,714	54.0
S. minima	3,956	6.3	4	0.1
S. decipiens	1,160	1.8	208	6.5
S. planctonis	1	<0.1	1	<0.1
S. macrocephala	1	<0.1	1	<0.1
P. draco	3,907	6.2	233	7.3
K. subtilis	468	0.7	97	3.1
K. pacifica	1,518	2.4	166	5.2
E. hamata	1	<0.1	0	0.0
E. fowleri	0	0.0	2	<0.1

Moore, 1949; Burfield, 1950), it seems to be maximally abundant in coastal areas where, according to Pierce (1951), the salinity is not less than 30‰ (Furnestin, 1952; Pierce, 1953; Bumpus and Pierce, 1955). The difference in relative abundance at the NG station, 10 miles from shore, and at the SL station, 40 miles from Miami, is striking (Table 1).

The seasonal maximum occurs in summer, and in both 1950 and 1951 it occurred in early August (Fig. 1a).

Sagitta hexaptera.—Rarely reported from the continental shelf area, *S. hexaptera* is mainly a species of the open oceans (Moore, 1949; Pierce, 1953; Bumpus and Pierce, 1955). Thus it was uncommon at the NG station and relatively abundant at SL 18 (Table 1).

Moore (*op. cit.*) states that the maximum occurs in summer or autumn, and in the Florida Current there were periods of abundance in the summers of 1950 and 1951 (Fig. 1b). There was also a distinct autumnal rise in 1950, which was followed by a decline and then a marked increase in December.

Sagitta lyra.—This is predominantly a species of the high seas. Pierce (1953), who reviewed the few records from the Atlantic Coast, recorded it as the least abundant species in collections off North Carolina. Moore (*op. cit.*) found it to be common at Bermuda but

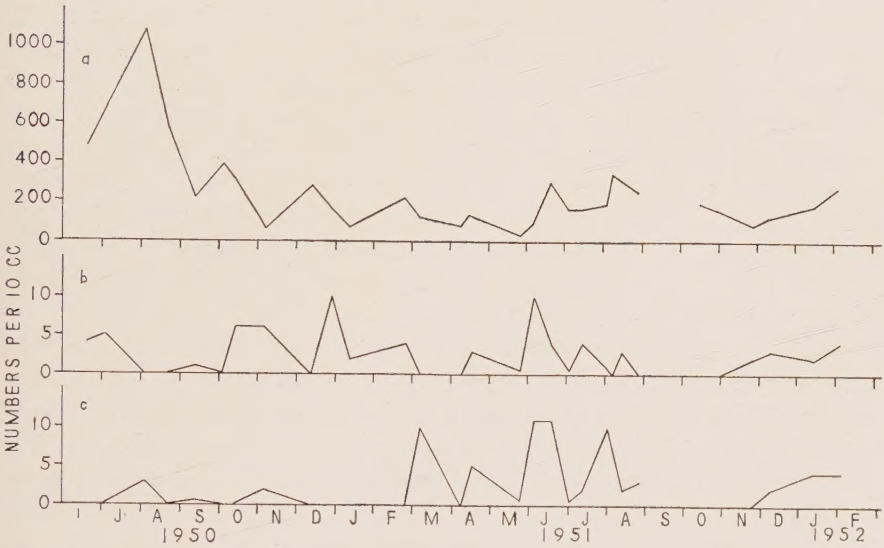

FIGURE 1. Seasonal variation in abundance of: a, *Sagitta enflata;* b, *S. hexaptera;* and c, *S. lyra.*

somewhat less so than *S. hexaptera.* Similarly, it was very rare at the NG station and comparatively commoner at SL 18, and it was less abundant than *S. hexaptera* at both stations (Table 1).

Moore (*op. cit.*) found a possible late summer maximum at Bermuda. At the NG station, it was most abundant in spring and summer (Fig. 1c), but its scarcity does not permit conclusions about a seasonal maximum.

Sagitta bipunctata.—Principally a common oceanic species in the North Atlantic (Moore, *op. cit.;* Pierce, 1953) and the eastern Mediterranean (Furnestin, 1953), it was moderately abundant at the NG station but rare at SL 18 (Table 1). There were summer and autumn maxima in 1950 and 1951 (Fig. 2a).

Sagitta hispida.—Since its description by Conant (1895), this species has been erroneously reported from many parts of the world (see the review of Pierce, 1951). Two recent reports, from the Red Sea, the Gulf of Aden and the Indian Ocean (Ghirardelli, 1948), and from the Calicut coast and the Gulf of Manaar (George, 1952), contribute to the confusion. Ghirardelli's specimens may have been *S. robusta* and those of George, *S. ferox,* both of which are quite similar to *S. hispida.* Tokioka (1955) states that, "*S. hispida* is confined to the

warm coastal waters along the eastern coast of the United States and the western coast of Africa (Rio de Oro) . . . ." It has also been recorded from coastal Jamaica and the Bahamas (Conant, 1896). It occurs abundantly in the harbor of Bimini, Bahamas, judging from a night surface tow supplied by H. E. Winn, in Biscayne Bay and in coastal waters off Miami. Further, it was numerous and the only chaetognath species present in a sample of Bermuda lagoon plankton obtained from W. H. Sutcliffe, Jr.; probably the Bermuda specimens recorded by Moore (1949) as *S. robusta* Doncaster, an Indo-Pacific species often confused with *S. hispida,* were in fact *S. hispida.*

Although never common, it was not a rare species at the NG station, and a few specimens were even collected at SL 18, one at 685 meters. These apparently constitute the first deep-water records. Since there was no indication of coastal influence at the NG station (Miller *et al.,* 1953), the Florida Current specimens are not thought to have originated in coastal waters of the Miami area. A theory of their origin is presented in the section on indicator species.

An autumn (October) maximum occurred in both 1950 and 1951, and in 1951, a spring maximum was also indicated (Fig. 2b).

Sagitta helenae.—This species has been reported from the waters off

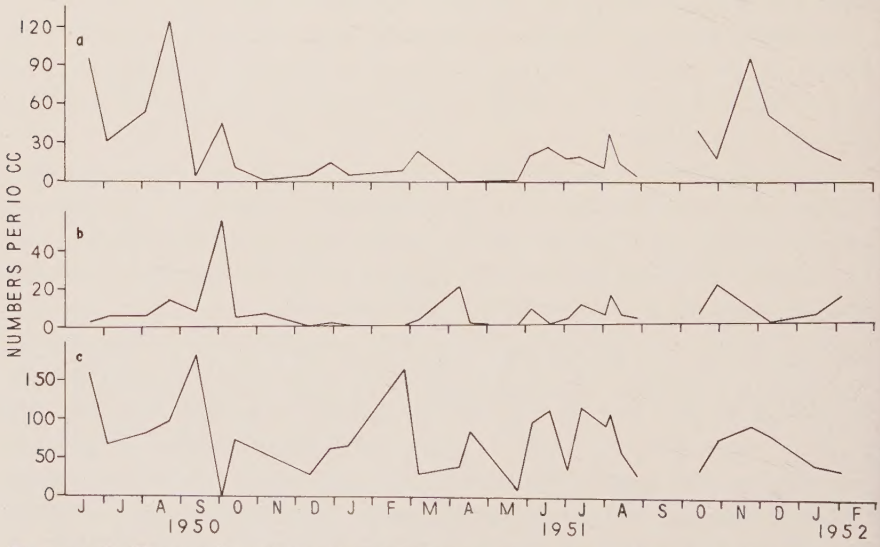

FIGURE 2. Seasonal variation in abundance of: a, *Sagitta bipunctata;* b, *S. hispida;* and c, *S. serratodentata.*

Bermuda (Moore, *op. cit.*), North Carolina (Pierce, 1953; Bumpus and Pierce, 1955), the west coast of Florida (Pierce, 1951) and Dry Tortugas (Ritter-Záhony, 1910). It also occurs inshore in the Miami area. At the NG station, it was collected sporadically and usually in small numbers (Fig. 4a); none were caught at SL 18.

Sagitta serratodentata.—This is a cosmopolitan oceanic species which, unlike *S. enflata,* is apparently more abundant in the open ocean than in coastal waters. It has been reported from various parts of the North American Atlantic coast (Pierce, 1953; Bumpus and Pierce, 1955), and at Bermuda it and *S. bipunctata* are the two most numerous of the smaller species of chaetognaths (Moore, *op. cit.*). Second in abundance at the NG station, it was the commonest species at SL 18 (Table 1).

Maximal numbers occurred in summer and autumn and, in addition, there was a winter maximum in 1951 (Fig. 2c).

Sagitta minima.—Recorded from the Atlantic, Pacific and Indian Oceans, between 40° N and 40° S (Ritter-Záhony, 1911a), *S. minima* is generally considered a coastal species (Thomson, 1948; Furnestin, 1952, 1953; Pierce, 1953). It has been reported in small numbers from oceanic areas (Germain and Joubin, 1916; Michael, 1919; Bollmann, 1932; and others); however Moore (*op. cit.*) did not find it in his Bermuda collections. At the NG station, *S. minima* was seldom absent and ranked third in total abundance, but it was very rare at SL 18. Its distribution off Miami shows that it, like *S. enflata,* is most abundant in the western edge of the Current, which here flows over the outer part of the continental shelf.

The seasonal maximum occurred in August (Fig. 3a).

Sagitta decipiens.—This is a cosmopolitan oceanic species (Ritter-Záhony, 1911a; Michael, 1919; Bollmann, 1932), which is probably most abundant in tropical and subtropical waters (Burfield and Harvey, 1926; Thomson, 1947). It was reported for the first time from the western North Atlantic during the course of the present study (Moore *et al.,* 1953). At the NG station, *S. decipiens* ranked sixth in total abundance (Table 1). It may be assumed to be present usually in this part of the Florida Current inasmuch as on the days it was not taken, the nets probably did not fish deeply enough (below 110 meters at the most) to catch this rather deep-living species. It was relatively much commoner at SL 18 than at the NG station.

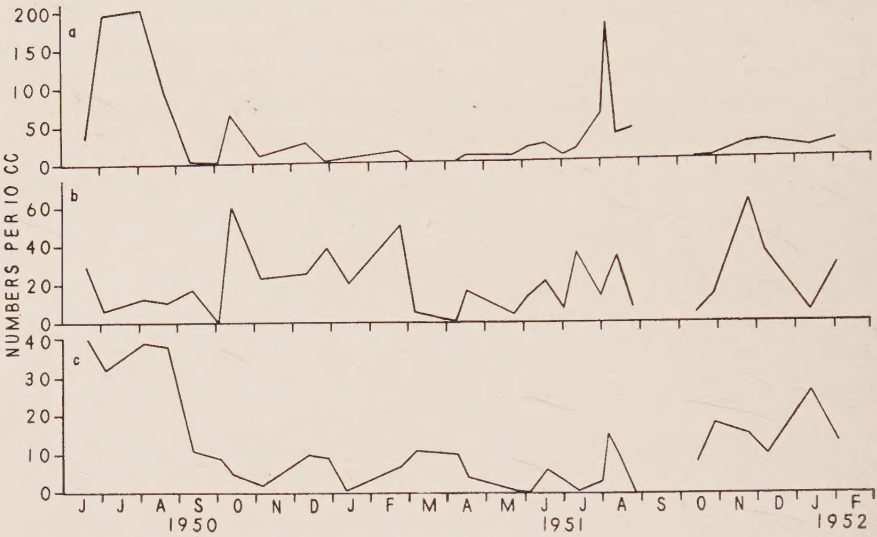

FIGURE 3. Seasonal variation in abundance of: a, *Sagitta minima;* b, *Pterosagitta draco;* and c, *Krohnitta pacifica.*

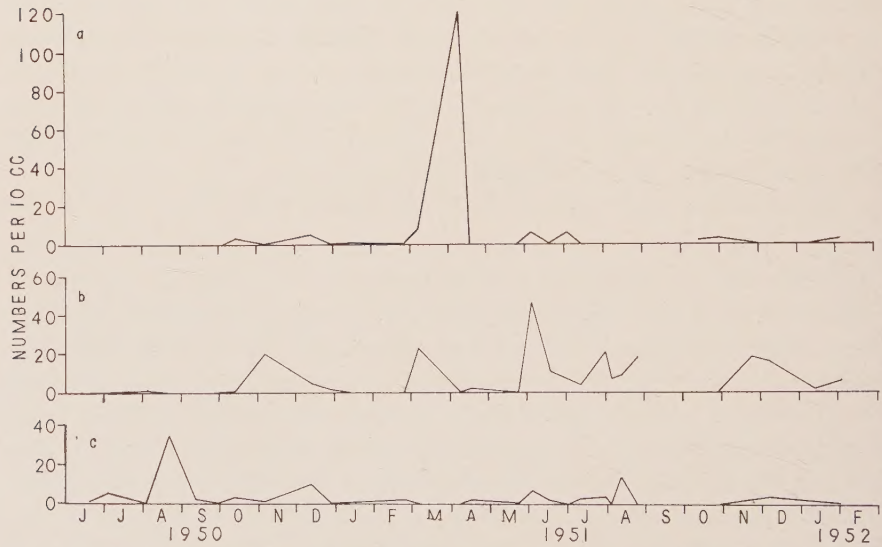

FIGURE 4. Seasonal variation in abundance of: a, *Sagitta helenae;* b, *S. decipiens;* and c, *Krohnitta subtilis.*

There were summer and autumn maxima at the NG station (Fig. 4b). *S. decipiens* was maximally abundant in early June, 1951; if a maximum occurred at that time in 1950, it was missed because there was no sampling then. On June 19, 1950, none were taken, probably because the sample was taken from shallow water (0-25 meters). A sharp decline in numbers was found on June 19, 1951. Although sampling extended only to 100 meters on that date, this may well represent a true decline for it was followed by a continuing downward trend in early and mid-July, when the nets fished as deep as 210 and 300 meters, respectively. The fall maximum occurred in November of both years.

Sagitta planctonis.—This species has not previously been recorded from the Atlantic coast of North America. One specimen was taken in a sample from 146-165 meters (NG 25D) and another from 731 meters (SL 18, C-8). Both were immature (Stage II).

Sagitta macrocephala.—No previous record of this species from the western North Atlantic is known to the writer. One specimen was caught at the NG station, between 192 and 292 meters (NG 16-18), and another at SL 18, at 713 meters (E-8). Fraser (1952) states that it is a warm (presumably meaning tropical), very deep water species like *S. planctonis* and often occurs with it.

Pterosagitta draco.—A cosmopolitan species in tropical and subtropical oceanic areas, *P. draco* has been recorded several times from the waters over the continental shelf of eastern North America (Huntsman, 1919; Bigelow, 1915, 1926; Bigelow and Sears, 1939; Pierce, 1953). In the Florida Current, it is a regularly occurring species which, along with *Sagitta minima,* was next in total abundance after *S. enflata* and *S. serratodentata* at the NG station. It was slightly more abundant at SL 18 (Table 1).

At Bermuda, *P. draco* is a fairly common species, with a maximum in autumn (Moore, 1949); an autumn maximum also occurred off Miami (Fig. 3b). In addition, a winter maximum was indicated by the February, 1951, sample and suggested in February, 1952, when sampling was concluded. Probably there is a period of generally high abundance from October or November through February, with a drop in January.

Krohnitta subtilis.—This is a species of tropical and subtropical oceans (Ritter-Záhony, 1911a; Bollmann, 1932; Thomson, 1947;

Furnestin, 1952). Along the eastern seaboard of North America, stray individuals have been taken over the outer edge of the continental shelf (Bigelow and Sears, 1939; Pierce, 1953; Bumpus and Pierce, 1955). By no means unusual in the Florida Current off Miami, *K. subtilis* was, however, never abundant. It was relatively commoner at SL 18 than at the NG station (Table 1).

The maximum occurred in August, with a winter maximum suggested in December (Fig. 4c). At Bermuda, where *K. subtilis* is fairly common, there was an autumn maximum (Moore, *op. cit.*). According to Moore (personal communication), there is a possibility that some of the Bermuda specimens were *K. pacifica.*

Krohnitta pacifica.—Probably because of confusion with *K. subtilis,* there have been very few records of *K. pacifica.* Thomson (*op. cit.*) and Tokioka (1939, 1940, 1951, 1952) have considered it an Indo-Pacific species. Specimens collected in the vicinity of Dry Tortugas and identified by Ritter-Záhony (1910) as *K. subtilis* were probably *K. pacifica.* However, the first Atlantic records known to the writer are those of Pierce from the Gulf of Mexico (1951) and from coastal waters and the Florida Current off North Carolina (1953).

It was considerably commoner than *K. subtilis* at both Florida Current stations (Table 1) and indeed was present on all but three of the 33 days of sampling at the NG station. Like *K. subtilis,* it was proportionately more abundant on the eastern than on the western side of the Current.

Figure 3c shows seasonal variation in abundance and a distinct summer maximum in 1950. The pattern of fluctuations in June, July and August, 1950, was almost exactly repeated during those months of 1951, only in lesser magnitude. However, the fluctuations in the months of October through January, 1950, differed entirely from those in the same months of 1951.

Eukrohnia hamata.—One specimen was taken at 250 meters (NG 4E) and another, between 225 and 275 meters (NG 30F). Counts and measurements of these specimens, respectively, are: length, 10 mm., 9.5 mm.; tail, 25 and 31 per cent; jaws, 9-9, 8-8; teeth, 11-?, 9-9. According to Fowler (1907), this species has not been recorded from water of a temperature higher than 12.7° C. The temperature at 213 meters the day one specimen (NG 30F) was taken was 7.4°C.

Eukrohnia fowleri.—Two specimens were caught at 590 meters (SL 18, E-7), where the temperature was 14.5°C. Subsequently two more were taken at the SL station, at 600 and 700 meters, and examined after two days in preservative. The ground color of the body was pale orange, and on each side there was a broad lengthwise band of brilliant orange chromatophores, especially and strikingly dark between the anterior end of the lateral fin and the neck and between the posterior end of the lateral fin and the caudal fin. Perhaps these areas are luminescent. Also there were clumps of chromatophores of the same intensity of orange scattered on the dorsal and lateral parts of the head and neck. The gut was bright orange.

One of the specimens was too poorly preserved to measure. Measurements of the remaining three are:

Length	Tail %	Jaws	Teeth
11.0 mm.	27	8-8	? (head mashed)
29.5 mm.	21	12-12	21-?
30.0 mm.	27	13-13	22-24

Whereas *E. hamata* was taken only at the NG station in relatively shallow, cold water, *E. fowleri,* described by Fraser (1952) as a warm (presumably meaning tropical), deep water species, was caught only at the SL station between approximately 600 and 700 meters. There are temperature records for two catches, 13.4°C at 600 meters and 14.5°C at 590 meters. Records at the SL station have shown that the temperature at 600 meters drops seasonally below 12°C and *E. hamata* may well occur there then and also in the deeper strata where 9.3°C (675 M) to 6.9°C (800 M) have been recorded.

Indicator Species

Using the typical T-S curves for Gulf of Mexico and Yucatán waters (Parr, 1935) and temperature and salinity data collected at the NG station, Miller *et al.* (1953) estimated the percentage of Gulf water present on most of the days of sampling (Fig. 5b). It was hoped that some species would be found to be definite indicators of either the Yucatán or Gulf component of the Current. Jones (1952) and Moore (1953), in studies of the Copepoda and Siphonophora, respectively, found only possible indicators except for one unfortunately rare siphonophore which appears to occur principally in Gulf water.

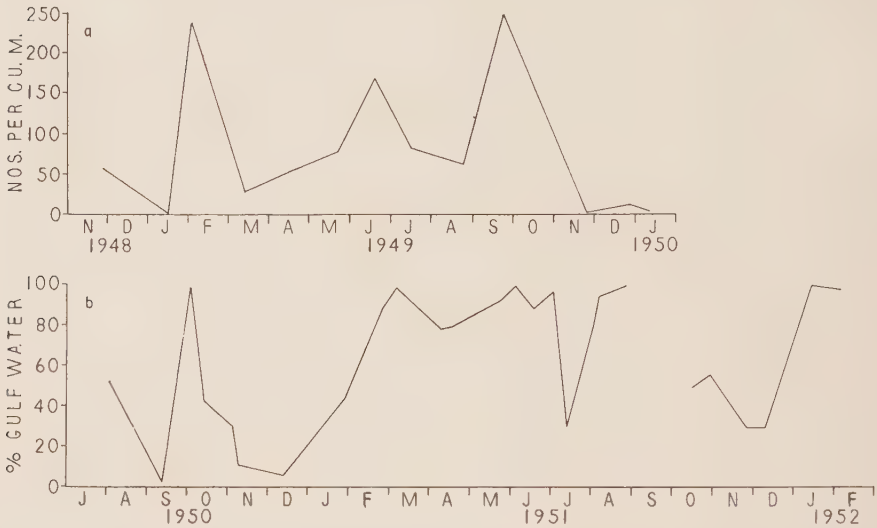

FIGURE 5. Seasonal variation in: a, abundance of *Sagitta hispida* off Cedar Key, Florida (from the data of Pierce, 1951); b, percentage of Gulf of Mexico water at the NG station from August, 1950, to February, 1952.

Concerning the Chaetognatha, no correlation was found between either the seasonal variation in abundance or the percentage abundance of any species relative to other species and the percentage of either Gulf or Yucatán water. Correlation coefficients were also calculated between various groupings of principally oceanic species (*e.g., Sagitta hexaptera, S. lyra, S. serratodentata, S. decipiens*) and the percentage of Yucatán water, and between principally neritic species (*e.g., S. hispida, S. helenae, S. minima*) and the percentage of Gulf water, but none were significant.

It was therefore decided to examine Pierce's (1951) data on seasonal variations in abundance of chaetognaths of inshore waters of the eastern Gulf with reference to circulation in the eastern Gulf and variations of the same species at the NG station. If certain assumptions are made, one species, *Sagitta hispida,* can be considered a possible indicator of Gulf water, although its absence would not necessarily indicate a low percentage or absence of Gulf water.

Sagitta hispida is a neritic species which prefers waters of low salinity (Pierce, *op. cit.*), and one would not expect to find it at all in the Florida Current. The fact that it does occur rather regularly

there, although in small numbers, indicates that it is carried into the Current by coastal water. However, the physico-chemical characteristics of the Current at the NG station are oceanic and there is no evidence that inshore east coast waters contribute to it at all (Miller *et al., op. cit.*). Since Pierce (1953) and Bumpus and Pierce (1955) did not report *S. hispida* from the Current off North Carolina, it appears that the species does not survive in appreciable numbers in the Current that far north and also that coastal waters along the eastern seaboard are not contributing it to the Current.

The first assumption is that the Current in its passage through the Yucatán Channel and the Straits of Florida does not pick up more than stray elements of coastal faunae on account of its physical nature (high temperature, high salinity) and its rapid rate of movement. However, the pilot chart of surface currents in June shows a clockwise eddy which abuts the northwest coast of Cuba and joins the Current as it sweeps through the Straits (Fig. 6). This could be a

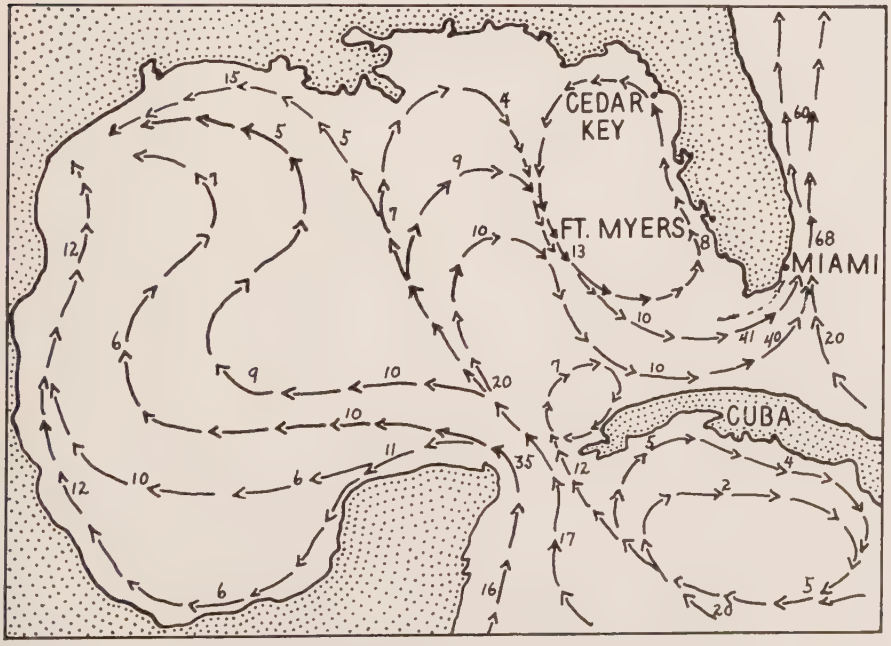

FIGURE 6. Surface ocean currents in the Gulf of Mexico in June, after Leipper (1954). Small numbers equal miles per day of current.

source of *S. hispida,* which occurs in Cuban coastal waters (Suárez Caabro, 1955).

Secondly, it is assumed that most or all of the specimens of *S. hispida* at the NG station come from the eastern Gulf of Mexico via coastal eddies. Pilot charts of surface currents in this area show a large counterclockwise eddy, a part of which flows southeasterly to join the Current as it passes through the Straits of Florida (Figs. 6 and 7). Although these are only estimates of currents, studies made by the Oceanography Section of the University of Miami Marine Laboratory confirm the general pattern of circulation figured. Neritic species picked up by this eddy must travel a great distance before reaching the Florida Current. On the basis of current velocities in June, it was crudely reckoned that an animal which entered the Gulf eddy off Fort Myers, Florida, would have been carried a distance of 1014 miles over a period of 98 days before reaching the NG station. If the animals originated in the Cedar Key area, the distance would be 814 miles and the time, only 73 days.

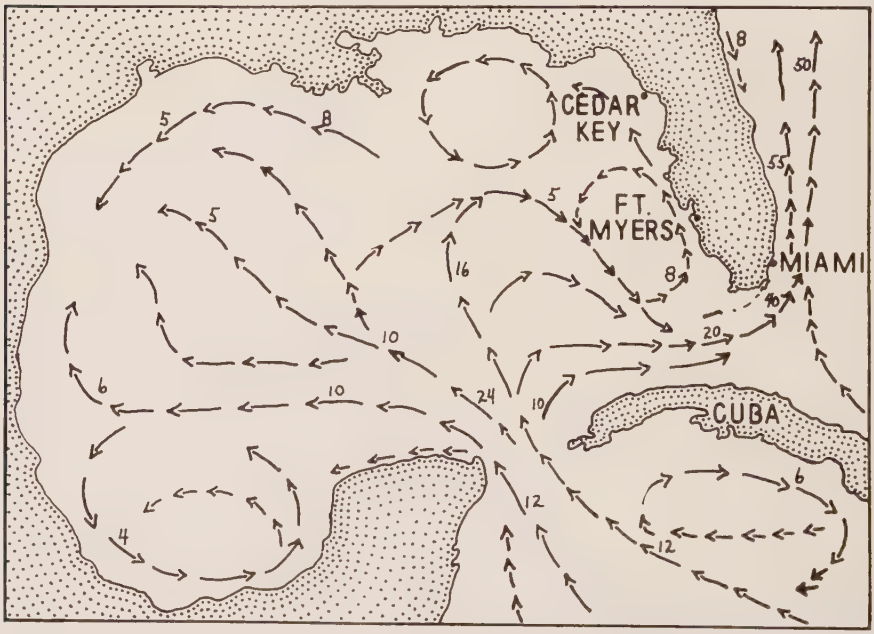

FIGURE 7. Surface ocean currents in the Gulf of Mexico in December, after Leipper (1954). Small numbers equal miles per day of current.

If the specimens of *Sagitta hispida* found in the Florida Current have originated in the Gulf, then the seasonal fluctuations in abundance at the NG station should reflect the fluctuations of the large populations which occur off the Gulf coast of Florida. Pierce (*op. cit.*) sampled these populations in three areas, at distances of one-half mile, five and fifteen miles from shore. The latter two stations should be in the northward-moving current (Frank Chew, personal communication); the area off Cedar Key would be the most likely of the three to furnish Florida Current specimens, on the basis of time. When the numbers of *S. hispida* per cubic meter at the two outermost stations off Cedar Key on each date of sampling are graphed, nearly equal maxima in February and September and a smaller peak in June are shown (Fig. 5a). The combined data from all three stations in all areas show that the maxima occurred during the same months and differed mainly in magnitude from those at the selected stations off Cedar Key. In the Florida Current, the spring and fall maxima followed after those off the west coast; there was no distinct summer maximum but a series of small increases in June, July and August (Fig. 2b). Possibly the periods of maximum abundance of *S. hispida* at the NG station were delayed expressions of the maxima which occurred off the west coast.

If most or all of the Florida Current specimens come from the Gulf, then there should be few or none present when the percentage of Gulf water is low. A comparison of the graphs of percentage of Gulf water (Fig. 5b) and numbers of *Sagitta hispida* (Fig. 2b) shows that this condition is generally fulfilled. There is close agreement between the two in October, 1950 and 1951, with the percentage of Gulf water rising and the numbers of *S. hispida* increasing, presumably as a result of the fall maximum on the west coast. There are two discrepancies, in September, 1950, and July, 1951. At those times, *S. hispida* may still have been so abundant after the summer maximum that even the low percentage of Gulf water was sufficient to insure its appearance in the Florida Current.

No direct correlation between abundance of *Sagitta hispida* and percentage of Gulf water would be expected because only a part of the eddy contributes to the Gulf component of the Current, according to the pilot charts, and because the animals picked up by the eddy presumably are part of the offshore fringe of the population. The species was, overall, most abundant at the one-half mile station in all three

areas sampled by Pierce *(op. cit.)*. Probably these animals suffer a certain mortality under oceanic conditions so that they appear in the Florida Current only after periods of especial abundance.

Vertical Distribution

Data on the vertical distribution of the commoner species were derived mainly from two sources, one a series of collections at the NG station with samples taken at four to six depths approximately at noon (Table 9) and the other a series of samples collected during the 24-hour period of July 1, 1953 at the SL station (SL 18) on the eastern side of the Florida Current about 40 miles from Miami (Table 10). At the latter location, the depth is in excess of 700 meters, in comparison with a depth of 300-400 meters at the NG station. The two locations also differ in that, from the western to the eastern side of the Current, the isotherms slope downwards very steeply. Thus, the 20°C isotherm occurs at 50 meters or less on the Miami side and at over 200 meters at Gun Cay or Cat Cay, the 15°C isotherm at approximately 100 meters off Miami in comparison with 500 meters on the other side, and so on (Sverdrup *et al.*, 1942, p. 674; Roane, 1954, Fig. 26).

From the NG series, the seasonal vertical distribution of 11 species was graphed (Part a of Figs. 10 through 19, Fig. 14b) and the 25, 50 and 75% levels and the spread of each were calculated. NG 27 and 38 were excluded from the latter calculations because samples were not taken deep enough to give a representative picture of distribution. These data are compared with those of Moore (1949) for six of the species *(Sagitta hexaptera, S. lyra, S. bipunctata, S. serratodentata, Pterosagitta draco* and *Krohnitta subtilis)* in the upper 300 meters at Bermuda. Moore (personal communication) also sampled Bermuda waters below 300 meters on two occasions, and he has kindly made his counts of the Chaetognatha available to the writer. These collections were made in daytime at several levels from the surface to 700 meters on May 28, 1940, and from the surface to 800 meters on July 31, 1940, and will be referred to, respectively, as *Culver* station 214 and *Culver* station 221.

From the results of the 24-hour station (SL 18), the vertical distribution of nine species was graphed (Part b of Figs. 10 through 13 and 15 through 19) to show diurnal movements, and the 25, 50 and 75%

levels and the spread calculated for comparison with those at the NG station and at Bermuda.

Mean Day-level and Spread. The terms mean day-level and spread were first used by Moore (1949), who defined mean day-level as the mean depth above which 50% of the individuals occurring in the upper 300 meters are found in the daytime, and spread as the difference in depth between the 25 and 75% levels of the population in the daytime. The values given here are means of the values for all the vertical distribution stations at which numbers are adequate and they were calculated by the method Moore (1955) described. The data obtained from all depths sampled at the SL station, not just those from the upper 300 meters, were used in calculating the levels there.

The term maximum, meaning that range of depth at which the greatest concentration of animals is found, has usually been employed in describing the vertical distribution of chaetognath species. Infrequently these figures have been qualified by reference to time *(e.g.,* Michael, 1911); usually they are rather wide ranges which indicate distribution only in general terms. In lieu of the average maximum, the mean 50% level or mean day-level has been used as a major reference point in the present study.

Excepting *S. enflata* and *S. bipunctata,* all of the species common to the Florida Current and Bermuda occupy a deeper day-level in the Florida Current (Table 2). Possibly the shallower levels of the two species can be explained on the basis of inadequate numbers. *S. enflata* is the most abundant species in the western side of the Current off Miami, while Moore recorded it only sporadically at Bermuda. Conversely, *S. bipunctata* is abundant at Bermuda and much less so off Miami.

Assuming that illumination and temperature together control the vertical distribution of chaetognaths, siphonophores and other kinds of zooplankton (Moore, 1953), differences in the depths of the isotherms and in transparency of water in the two areas may be responsible for the generally lower mean day-levels of the species at the NG station. Since Moore *(op. cit.)* found that the regression of change in level of the 15°C isotherm on change in level of various species of Siphonophora is 95%, this isotherm was selected for comparison by Roane (1954). Roane compared the mean annual level of this isotherm in Bermuda, using the data of Iselin (1936), with that at the NG station (Miller *et al., op. cit.)* and found that the mean depth at the former

TABLE 2

MEAN DAY-LEVELS, 50 PER CENT LEVELS AND SPREADS OF CHAETOGNATHA FROM THE NG AND SL STATIONS AND BERMUDA (FIGURES IN METERS).

Species	NG md-1[1]	BDA[2] md-1	SL 50% 1[3]	SPREAD NG	SPREAD BDA	SPREAD SL
S. enflata	88	115	276	74	180	98
S. hexaptera	109	95	301	78	105	144
S. lyra	179	120	605	70	85	67
S. bipunctata	79	95	—	55	105	—
S. hispida	89	—	—	81	—	—
S. serratodentata	100	75	303	80	70	255
S. minima	109	—	—	71	—	—
S. decipiens	176	—	473	96	—	385
P. draco	99	65	302	84	80	243
K. subtilis	150	135	220	77	95	427
K. pacifica	63	—	306	52	—	200

[1]mean day-level
[2]Bermuda
[3]50% level in "noon" (1030-1355) series, to 713 M., of SL 18

locality was 608 M and, at the latter, 151 M. From this, there is no indication that temperature is the factor which makes for the deeper levels at the NG station. On the other hand, the average extinction coefficient was found to be 0.062 (Miller *et al., op. cit.)* in comparison with 0.075 at Bermuda (Hela *et al.,* 1953). Until additional hydrographic and biological information make a more complete explanation possible, it is assumed that mean day-levels are deeper at the NG station because light penetrates deeper.

The mean day-levels of the eight species common at both NG and SL stations occur in the same relative order of depth in the two areas, with the exception of *Krohnitta subtilis* and *K. pacifica,* which essentially exchange places (Table 2, Fig. 8). At both localities, the mean day-level of *Sagitta enflata* is second in occurrence and below it, there is a group of species. the levels of which are within 10 M of one another. At the NG station, this group consists of *Pterosagitta draco, S. serratodentata* and *S. hexaptera,* and the same species, with the addition of *K. pacifica,* occur together at the SL station. *S. decipiens* and *S. lyra* follow in the same order in both localities but are far more widely separated at the SL station.

The great increment in depths of the 50% levels at the SL station over those at the NG station is probably a result of the steep downward

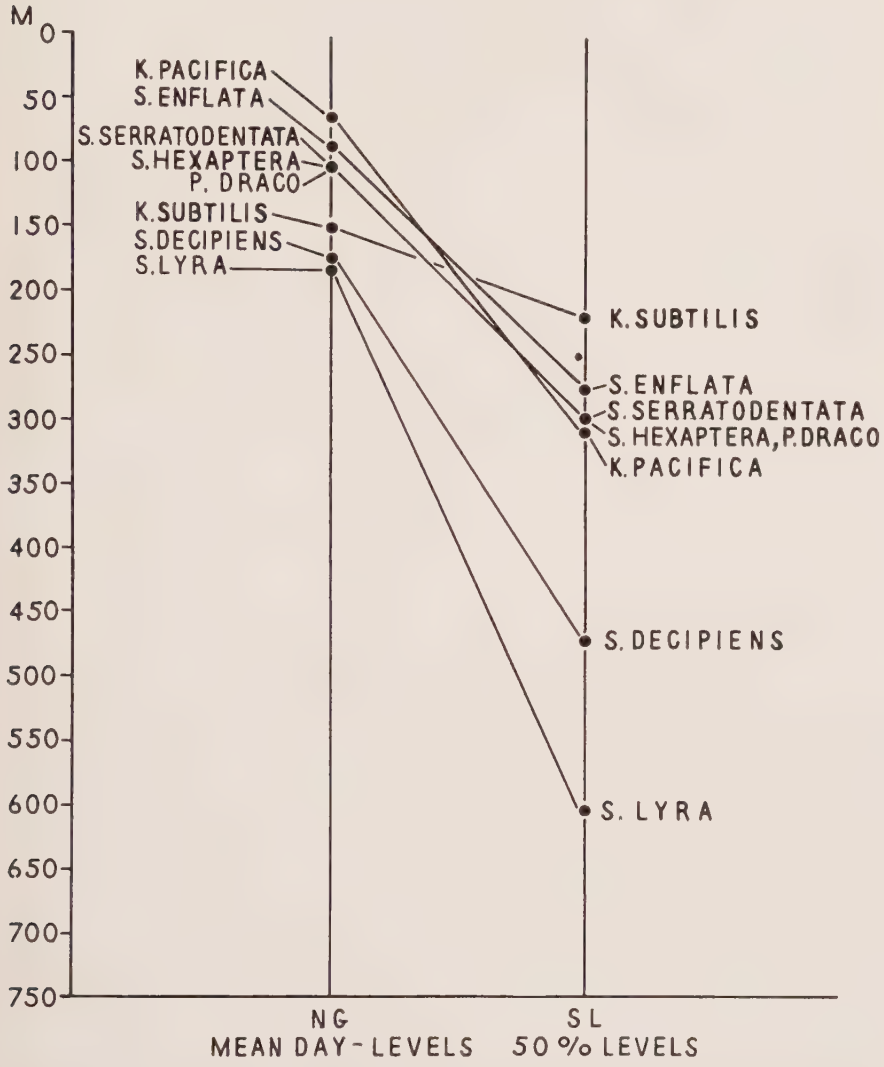

FIGURE 8. Comparison of depths of mean day-levels at the NG station with depths of 50 per cent levels at the SL station.

slope of the isotherms from the western to the eastern side of the Current. The mean temperatures corresponding to each mean day-level at the NG station are compared with temperatures at the 50% levels at the SL station in Table 3. In discussing the effect of tem-

perature on vertical distribution, the term optimum will be used for convenience to indicate the approximate temperature at which a population of chaetognaths tends to congregate. As yet, there are no precise data on the temperature requirements of these species and it is especially desired that reference to the optimum not imply such data.

TABLE 3

MEAN TEMPERATURES (°C) AT NG MEAN DAY-LEVELS COMPARED WITH TEMPERATURES AT 50 PER CENT LEVELS AT SL 18.

NG		SL	
Species	°C	Species	°C
Krohnitta pacifica	24.3	*Krohnitta subtilis*	21.8
Sagitta enflata	19.9	*Sagitta enflata*	19.9
Pterosagitta draco	18.9	*S. hexaptera*	19.4
S. serratodentata	18.8	*Pterosagitta draco*	19.4
S. hexaptera	17.1	*S. serratodentata*	19.4
K. subtilis	16.2	*K. pacifica*	19.3
S. decipiens	13.7	*S. decipiens*	17.4
S. lyra	12.5	*S. lyra*	14.2

Within the limits imposed by the fact that the SL data represent only one day, it seems clear that temperature is a major factor responsible for the deeper SL 50% levels. *S. enflata* was found at the same temperature at both localities (Table 3) and its SL 50% level was 188 M. deeper than the mean day-level at the NG station (Table 2). Excepting *K. pacifica,* the 50% levels of the other species occurred in water warmer by 0.5 to 5.6°C. If temperature were the only physical factor influencing vertical distribution around noon and if the mean temperatures of the mean day-levels at the NG station were optimal, or nearly so, for this time of day, then one would expect to find the 50% levels of most of the species at even greater depths on the eastern side of the Current. By combining the effect of light with that of temperature, one can, in a general way, account for the differences in depth of the 50% and mean day-levels of those species found in the euphotic zone at midday.

Since most of the species were found at a warmer level in the deeper column of water, these temperatures rather than those at the NG station may be closer to the midday optima. If this is so, then some factor or combination of factors must be forcing these species in the shallower water column on the western side away from their optima into colder water. That illumination is such a factor is likely; the

possibility of a correlation between deviations of the mean day-level of the species of Chaetognatha grouped together and deviations in the depth of the 10^{-2} isolume has been found by Moore *et al.* (1953).

The 50% levels of the deepest-living species, *Sagitta decipiens* and *S. lyra,* are comparatively widely separated in depth (132 M) and temperature (3.2°C) at the SL station, but at the NG station, their mean day-levels are separated by only three meters and 1.2°C. Apparently both species tend to congregate at a low level of illumination; in fact at the SL station, their 50% levels were in the "aphotic" zone. Since these levels were in deeper and warmer water in the deeper water column at the SL station (Fig. 8, Table 3), these conditions may be closer to the midday optima of the animals than those at the NG station, and it may well be that at the latter locality reaction to light causes the animals to congregate at depths where temperatures are lower than their optima. On the other hand, another factor, possibly pressure, as postulated by Moore *et al. (op. cit.)* and Moore (1955), may deter them from going deeper to cooler temperatures at the SL station. If conditions at the midday levels at SL 18 are closer to the optima than those at the NG station, then one might expect the two species to be more abundant in the eastern part of the Current. A comparison of samples taken at NG 16, a 24-hour station, with those from SL 18 in percentage of the total chaetognath catch shows that both species were more abundant at the SL station, *S. decipiens* forming 2.0% at NG 16 and 6.5% at SL 18, and *S. lyra,* 0.4% at NG 16 compared with 2.1% at SL 18.

The 50% level of *Krohnitta pacifica,* a shallow-living, warm-water species at the NG station, occurred in much deeper, colder water at the SL station (Tables 2 and 3). The levels of *K. subtilis* were also quite different at the two locations, but the differences, compared with those of *K. pacifica,* are reversed, the 50% level of *K. pacifica* having occurred in water 5.0°C colder and that of *K. subtilis,* 5.6°C warmer on the eastern than on the western side. Again it seems reasonable to conclude that both species can find optimal combinations of temperature and light in the deeper water column. It is inferred that *K. subtilis* is less tolerant of light than *K. pacifica* and that at the NG station, the level of low illumination selected is in water colder than the midday optimum.

The values for spread (Table 2) can be taken as an index of the vertical diffuseness of the populations. Comparing the values at the

TABLE 4

MEAN LEVELS AT THE NG STATION AND LEVELS AT SL 18. FIGURES IN METERS.

Species	NG					SL 18				
	25%	50%	75%	Spread	Range	25%	50%	75%	Spread	Range
Sagitta enflata	53	88	127	74	0-350	227	276	325	98	0-713
S. hexaptera	86	109	164	78	0-350	246	301	390	144	0-731
S. lyra	147	179	217	70	0-350	571	605	638	67	119-713
S. bipunctata	51	79	106	55	0-350	—	—	—	—	0-713
S. hispida	38	89	119	81	0-350	—	—	—	—	0-685
S. serratodentata	65	100	145	80	0-350	234	303	489	255	0-713
S. minima	76	109	147	71	0-350	—	—	—	—	119-302
S. decipiens	117	176	213	96	0-350	206	473	591	385	59-731
Pterosagitta draco	62	99	146	84	0-350	237	302	480	243	0-731
Krohnitta subtilis	112	150	189	77	0-350	165	220	592	427	0-731
K. pacifica	42	63	94	52	0-292	251	306	451	200	0-601

NG station with those for the same species at Bermuda (Moore, 1949), the latter are all greater except for *S. serratodentata* and *P. draco*. If the penetration of light is greater or the temperature lower in one area compared with another, theoretically the spread will be less (Moore *et al.*, 1953). There are no temperature data available for the Bermuda vertical distribution station, but, as stated above, the average extinction coefficient of Bermuda water is greater than that at the NG station. As in the case of the generally deeper Florida Current mean day-levels, the lesser spreads of most of the species are assumed to be at least partly a result of deeper penetration of light. It should also be noted that, while the Bermuda material was obtained from the surface to 300 M and is thus comparable in range to the NG samples, the total depth at the Bermuda station is approximately 500 fathoms; and waters of 10°C and colder are doubtless separated by a greater distance from the warm upper layers at Bermuda than at the NG station where this temperature may be encountered at 200 M.

The spreads at the SL station were also greater than those at the NG station for all species except *S. lyra*, for which the value was about the same (Table 2). Accompanying the shallowness of the water column at the NG station is the compression of the isotherms relative to their distribution at the SL station, as noted earlier. The depths of the isolumes can be assumed to be about the same at both locations. It is obvious, however, that the combined conditions of temperature and illumination at any depth, except the upper few meters, at the NG station are considerably different from those at corresponding depths at the SL station. These conditions appear to compress the populations of chaetognaths *(i.e.,* the spreads of most species are less) to varying degrees.

Mean levels at the NG station, percentage levels at SL 18, spreads and depth ranges are summarized in Table 4, and the temperatures at these depths, in Table 5.

Seasonal Vertical Distribution; Diurnal Migration. The vertical distribution of each species present in adequate numbers on eight occasions between January 12, 1951, and January 14, 1952, is given subsequently, together with data showing patterns of diurnal movement at station SL 18. The known temperature ranges of the species in the Florida Current and records of other workers are included.

Sagitta enflata. Usually considered epiplanktonic (Kuhl, 1938; Furnestin, 1952), this species has been taken as deep as 3,000 meters

TABLE 5
MEAN TEMPERATURES (°C) AT MEAN NG LEVELS AND TEMPERATURES AT SL LEVELS.

Species	NG			SL			
	25%	50%	75%	25%	50%	75%	Range
Sagitta enflata	22.6	19.9	16.9	21.6	19.9	19.0	22.6-16.9
S. hexaptera	19.1	17.1	14.0	21.0	19.4	18.1	21.0-14.0
S. lyra	14.3	12.5	11.4	15.0	14.2	13.2	15.0-11.4
S. bipunctata	22.5	20.6	19.1	—	—	—	22.5-19.1
S. hispida	24.5	19.5	17.5	—	—	—	24.5-17.5
S. serratodentata	21.5	18.8	15.5	21.4	19.4	16.6	21.5-15.5
S. minima	21.7	18.9	15.8	—	—	—	21.7-15.8
S. decipiens	16.8	13.7	12.8	22.4	17.4	14.4	22.4-12.8
Pterosagitta draco	21.9	18.9	15.9	21.3	19.4	16.8	21.9-15.9
Krohnitta subtilis	21.1	16.2	12.8	24.0	21.8	14.4	24.0-12.8
K. pacifica	25.7	24.3	21.5	20.7	19.3	17.2	25.7-17.2

(Germain and Joubin, 1916). At the NG station, most of the animals occurred in the upper 200 meters, within which distribution was variable (Figure 9a).

Figure 9b shows vertical distribution during a 24-hour period at station SL 18 and clearly indicates diurnal migration. Owing to the failure of the depth-distance recorder in the series from 1925 to 2030 hours (SL 18-F), the numbers per mile are not known. However, the nets at the five levels fished for approximately the same amount of time, and the percentage of the total count at each level is graphed as a rough indication of distribution. Continued downward movement after midday and the accumulation of the majority of animals below 500 meters is noteworthy (Figure 9b, 1505-1810 hours); in the same period, distribution of *S. hexaptera* (Figure 10b), *Pterosagitta draco* (Figure 16b) and *Krohnitta subtilis* (Figure 17b) are similar. Although the sampling between 1925 and 2030 hours did not go deep enough to give a good picture of distribution, a considerable increase was found in number of animals in surface waters.

S. enflata has been recorded as abundant in water of approximately 13.5 to 24.5°C (Thomson, 1947) and of 25° C and higher (Kuhl, 1938); mean temperatures of the levels in the Florida Current fall within this range (Table 5). The known extremes at which it was taken, however, were 7.9°C (NG 30, 25 per cent level) and 27.6°C (SL 18, D-0).

Sagitta hexaptera. At the NG station, this uncommon species occurred principally in the upper 150 meters (Figure 10a) whereas at station

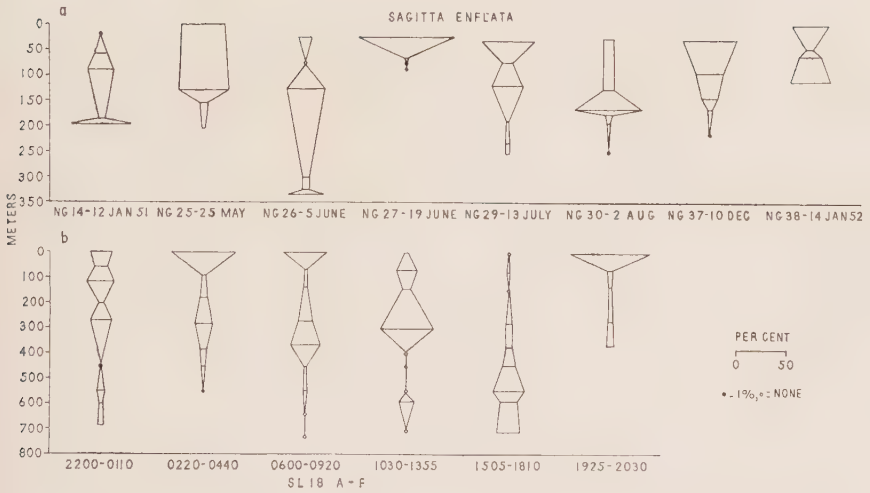

FIGURE 9. *Sagitta enflata:* a, seasonal variation in vertical distribution at the NG station; b, diurnal vertical distribution at SL 18.

SL 18, it was found in good numbers through a much greater vertical range (Figure 10b, Table 4). In the *Culver* station series off Bermuda, it was taken as deep as 800 meters, but the maximum level was in the upper 100 meters (H. B. Moore, personal communication).

The pattern of seasonal vertical distribution at the NG station (Figure 10a) was similar to that found by Moore (1949) except in December when over 50 per cent of the catch were found at the surface at Bermuda.

Moore *(op. cit.)* found slight diurnal migration, chiefly of the population in the upper 25 meters, and no night increment from below 250 meters. The data from station SL 18 (Figure 10b) show diurnal migration and night increment from below 250 meters, although this is not as marked as in *S. enflata.*

The temperature range of the maximum level is recorded as 20-25°C by Kuhl (*op. cit.*). Thomson (*op. cit.*) gives a total range of 11-24°C with the animals abundant only between 15 and 22°C. While the known extremes in the Florida Current (7.5°C, 75 per cent level, NG 32 - 27.6°C, SL 18, D-0) exceed this range, the means for the levels (Table 5) fall within it.

Sagitta lyra. Moore *(op. cit.)* reviewed the literature on the vertical distribution of this species, the maximum of which has usually been

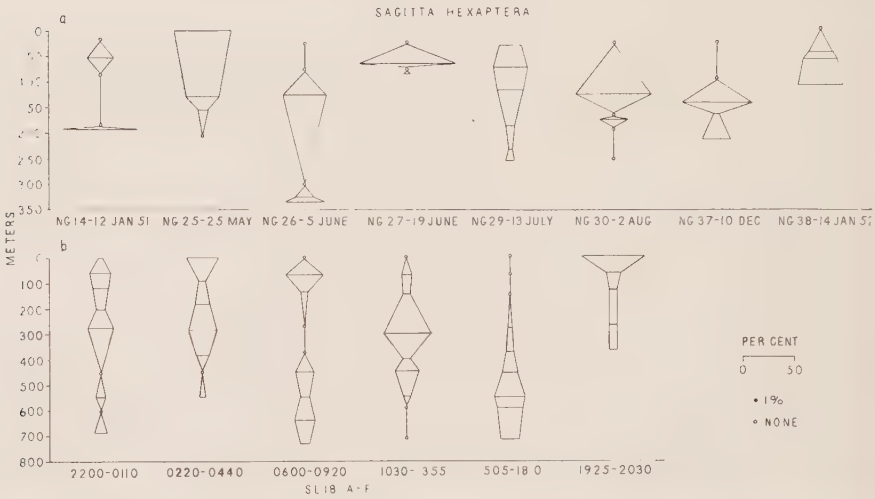

FIGURE 10. *Sagitta hexaptera:* a, seasonal variation in vertical distribution at the NG station; b, diurnal vertical distribution at SL 18.

recorded as below 100 meters. In Bermuda, on five of the eleven dates of sampling, the maximum occurred in the upper 100 meters; it was below 100 but usually above 200 meters on the remaining dates (Moore, *op. cit.).* However, in the two deeper series of samples *(Culver* stations), the maxima were, on May 28, 1940, and on July 31, 1940, respectively, nearly uniformly spread between 150 and 400 meters, and between 350 and 400 meters (H. B. Moore, personal communication). On the other hand, while *S. lyra* is not common at the Great Barrier Reef, nearly five times as many specimens were taken at a position within the reef with a depth of approximately 32 meters than at stations outside the reef where depths from 250 to 500 meters were fished (Burfield, 1950).

At the NG station, the distribution is similar to that at Bermuda, although generally somewhat deeper (Figure 11a). *S. lyra* was found only once at the surface (NG 39 A). In June and January, the only specimens taken were juveniles, in the upper 100 meters, a circumstance which may be comparable with the large concentrations, perhaps spring and winter broods, found at the surface at Bermuda in May and December.

Moore *(op. cit.)* found little diurnal migration, and that occurring chiefly in the upper 25 meters, with no night increment from below

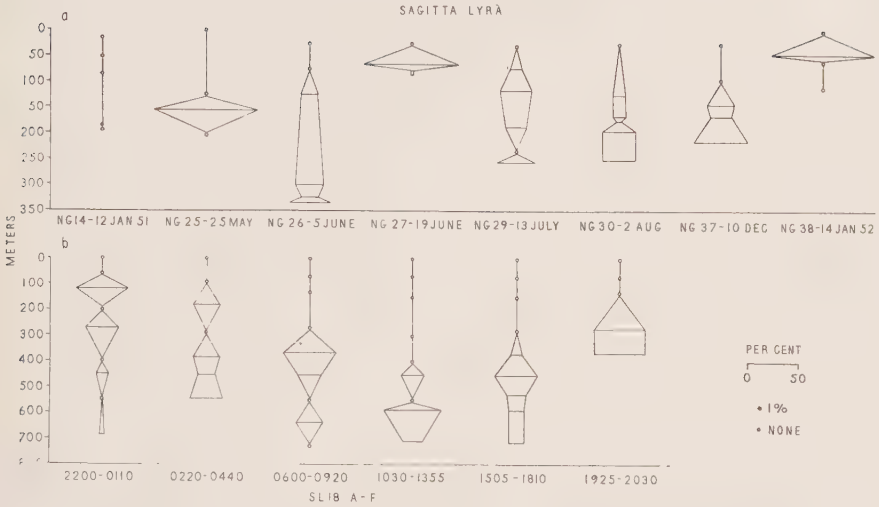

FIGURE 11. *Sagitta lyra:* a, seasonal variation in vertical distribution at the NG station; b, diurnal vertical distribution at SL 18.

250 meters. At the SL station, a marked diurnal rhythm was found (Figure 11b). The night increment in the upper 250 meters came entirely from below 250 meters and in fact from below 400, if the midday series (1030-1355 hours) is taken to represent the daytime distribution.

Thomson (*op. cit.*) gives a range of approximately 6 to 21°C which is close to the extremes at which *S. lyra* was found in the Florida Current: 6.3 (?-interpolated) to 22.5° C. The range of mean temperatures at the levels was smaller and lower than that of any other of the more abundant species (Table 5).

Sagitta bipunctata. This species is generally considered epiplanktonic (Moore, *op. cit.*). Burfield (1950) stated that it is found from the surface to 50 meters, and, in the Mediterranean, Furnestin (1952) took 98 per cent of the total catch in surface hauls. However, at *Culver* station 214, it occurred from the surface to 700 meters (except for the tow between 550 and 600 meters), with a distinct maximum between 50 and 100 meters; at station 221, it was present in all hauls from the surface to 800 meters, and the majority of specimens was taken between 50 and 200 meters (H. B. Moore, personal communication). Although the level of maximum abundance both at Bermuda and in the Florida Current (Figure 12a) was always in the upper 200 meters

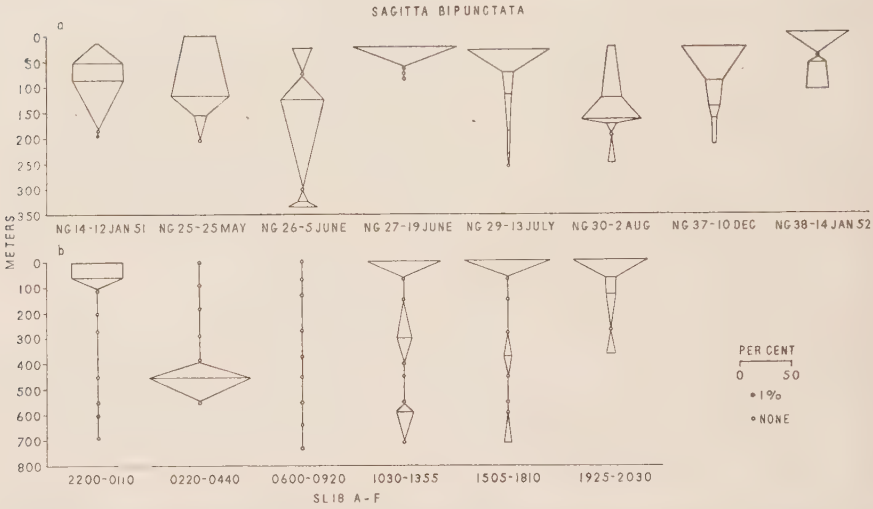

FIGURE 12. *Sagitta bipunctata:* a, seasonal variation in vertical distribution at the NG station; b, diurnal vertical distribution at SL 18.

and sometimes in the upper 50, the species is by no means strictly epiplanktonic.

Data on vertical distribution at the SL station (Figure 12b) were too few to show diurnal movements, if any.

The temperature range of the level of maximum abundance has been recorded as 15 to 25°C (Kuhl, *op. cit.*), and the total range as 11 to 24°C (Thomson, *op. cit.*). A considerably greater range, 7.8 to 28.4°C was found at the NG station. Mean temperatures (Table 5) are within the previously published ranges.

Sagitta hispida. The vertical distribution at the NG station (Figure 13a) was irregular, and the data show only that the population was generally concentrated in the upper 200 meters. A rare species at the SL station, it was taken at the surface and also as deep as 685 meters.

There is no information on diurnal migration by this species.

S. hispida was taken in water ranging from 7.9 to 28.0° C. The mean temperatures at its mean levels are given in Table 5.

Sagitta serratodentata. Moore (1949) reviewed the records of vertical distribution and found conflicting statements, with the day maximum given as near the surface, at 400 meters, and about 1,200 meters. Furnestin (1952) stated that, in the Mediterranean, ". . . *S. s. atlantica*

moves from the deep strata towards the superficial water layers during the night and ought to be considered as mesoplanktonic." At *Culver* station 214, it was present in all hauls, except between 550 and 600 meters, from the surface to 700 meters, and the maximum occurred between 50 and 100 meters; at station 221, it was taken in all hauls from the surface to 800 meters, excepting the 600 meter haul, and the maximum, although much less clearly marked, again fell between 50 and 100 meters (H. B. Moore, personal communication).

FIGURE 13. Seasonal variation in vertical distribution at the NG station: a, *Sagitta hispida;* b, *S. minima.*

Records of distribution at the NG station (Figure 14a) show only that the level of maximum concentration was somewhere above 200 meters, and the same is true of Moore's data, although on most dates the maximum was just short of 100 meters. In contrast to these data is the much deeper 50 per cent level of this species at the SL station (Table 2). The level of the maximum apparently varies considerably with the area and time of year.

Definite diurnal migration was found in the Florida Current (Figure 14b) as in Bermuda, where Moore *(op. cit.)* stated that it occurred mostly in the upper 50 meters. At SL 18, the large night surface population remained at the surface well into the morning, and, although the majority retreated at midday, a small number remained all the

time. None of those collected from the surface at midday were mature (two in stage III, three stage II, one stage I, two juveniles, and three stage I or II).

Like *Sagitta enflata* and *S. hexaptera, S. serratodentata* was oddly distributed in late afternoon (1505-1810 hours). The numbers at the surface were over twice the midday figure, but the percentage of the total catches present in the upper 150 meters was less than at midday. The level of maximum abundance had moved down from 302 meters, and 75 per cent of the population was rather uniformly spread between 375 and 713 meters. There appears to have been a generally continuing downward movement with diminishing light intensity.

The extremes of temperature at which the species was collected were 7.6°C and 27.6°C. The mean temperatures (Table 5) are within the range of 15 to 25°C given for the maximum level by Kuhl *(op. cit.). Sagitta minima.* As is the case with most species, records of depth distribution vary. It has been reported as epiplanktonic (Ritter-Záhony, 1911; Germain and Joubin, 1916; Ghirardelli, 1950, 1952; Furnestin, 1952, 1953), ranging from the surface to the limit of light (Ritter-Záhony, 1911a), and as a deep-living form of cool tropical waters, with a range of 0 to 300 meters (Kuhl, 1938). Off southeastern Australia, Thomson (1947) found it numerous in the upper 50 meters and abundant from 50 to 500 meters.

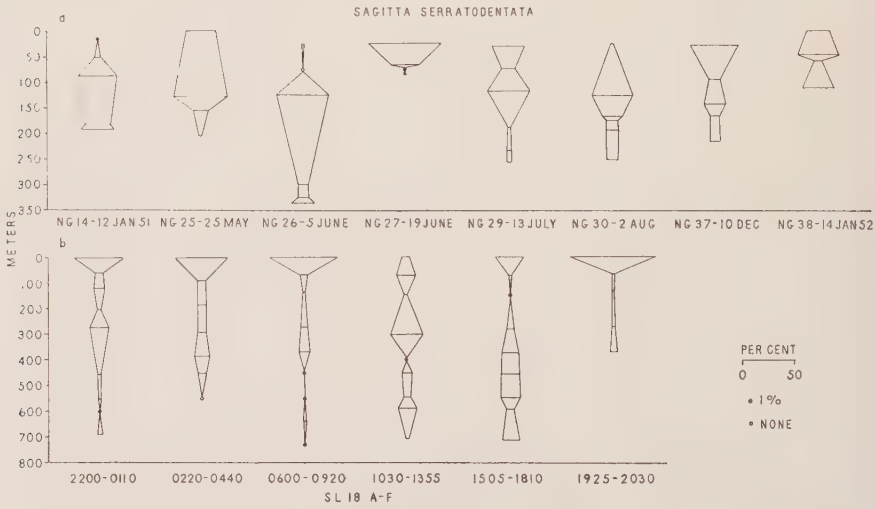

FIGURE 14. *Sagitta serratodentata:* a, seasonal variation in vertical distribution at the NG station; b, diurnal vertical distribution at SL 18.

At the NG station, the maximum usually occurred between 100 and 200 meters and twice was in the upper 100 meters (Figure 13b). Since the species was uncommon at the SL station, where it was collected between 119 and 302 meters, there are no data on diurnal migration.

The extremes of temperature at which it was taken at the NG station were 7.6 and 27.0° C. Mean temperatures at the mean levels are given in Table 5.

Sagitta decipiens. A species of the lower epiplankton and the mesoplankton (Ritter-Záhony, 1911, 1911a; Michael, 1919; Furnestin, 1952), it has been reported to have a range of maximum level from 100 to 600 meters (Bollmann, 1932) and 200 to 600 meters (Kuhl, *op. cit.).* Thomson (1947) found it rare in the upper 50 meters, numerous from 50 to 100 and abundant from 100 to 500 meters.

The maximum was usually below 100 meters at the NG station (Figure 15a). The surface maximum on May 25 consisted of very few specimens, and, on the days (June 19 and January 14) when the maximum was in the upper 100 meters, the nets scarcely fished deeper. However, considering all NG data, *S. decipiens* was at times relatively abundant in the upper 50 and 100 meters.

There is slight evidence of diurnal migration (Figure 15b), with a downward trend apparent between 0220 and 0920 hours. At midday, however, the upper part of the population had moved upwards over 100 meters so that it was almost as shallow as at midnight. The late afternoon distribution is somewhat similar to that found for *S. enflata* and *S. hexaptera.*

The range of temperature at the maximum has been recorded as 4.5 to 15.5°C (Bollmann, 1932) and the total range (off southeastern Australia), as approximately 11 to 22°C. The total range at the NG station was greater: 7.4 to 23.4° C.

Pterosagitta draco. This is considered an epiplanktonic species (Ritter-Záhony, 1911, 1911a; Michael, 1919; Ghirardelli, 1948, 1950; Burfield, 1950), with the maximum in the upper 100 meters (Bollmann, 1932; Kuhl, 1938). It has been collected as deep as 5,000 meters (Germain and Joubin, 1916). In the Florida Current, however, the maximum occasionally occurred between 100 and 150 meters at the NG station and was below 300 meters three times during the 24-hour period of SL 18 (Figure 16).

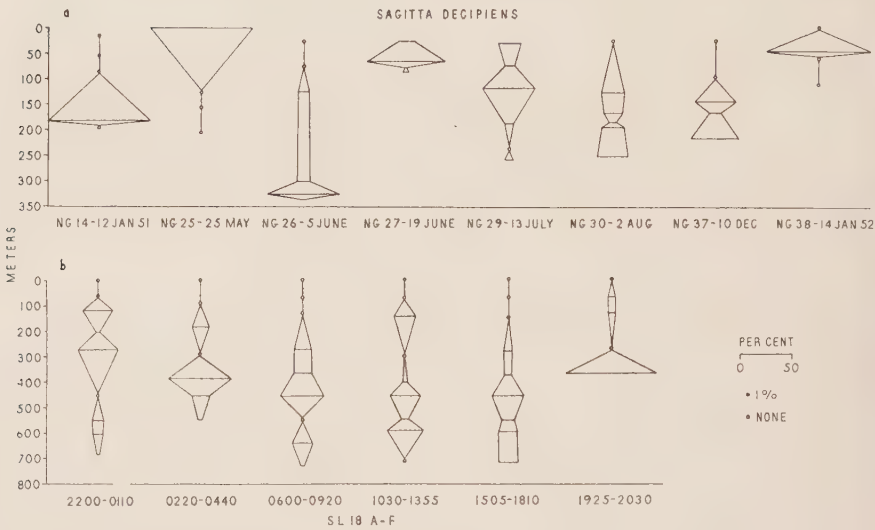

FIGURE 15. *Sagitta decipiens:* a, seasonal variation in vertical distribution at the NG station; b, diurnal vertical distribution at SL 18.

The data on vertical distribution (Figure 16a) were, on comparable dates, similar to that from Bermuda (Moore, *op. cit.*), and marked diurnal migration found at Bermuda also occurred at the SL station (Figure 16b).

The temperature range (Table 5) of this species in the Florida Current falls within those previously recorded: 18-25° C for the maximum level (Kuhl, *op. cit.)* and approximately 12-23° C total range (Thomson, *op. cit.).*

Krohnitta subtilis. As is usually the case, records of vertical distribution vary considerably. Michael (1911) gave 400-500 meters as the depth of the maximum and Kuhl *(op. cit.),* 50-100 meters. At Bermuda the maximum always occurred in the upper 200 meters, occasionally in the upper 100, but at both stations in the Florida Current, it frequently occurred below 200 meters (Figure 17).

Evidence indicating slight diurnal migration was found (Figure 17b).

Thomson *(op. cit.)* recorded *K. subtilis* from waters of 7.5 to 22.5° C but found it to be numerous only between approximately 14.5 and 20.5° C. The range for the maximum level given by Kuhl *(op. cit.)* is

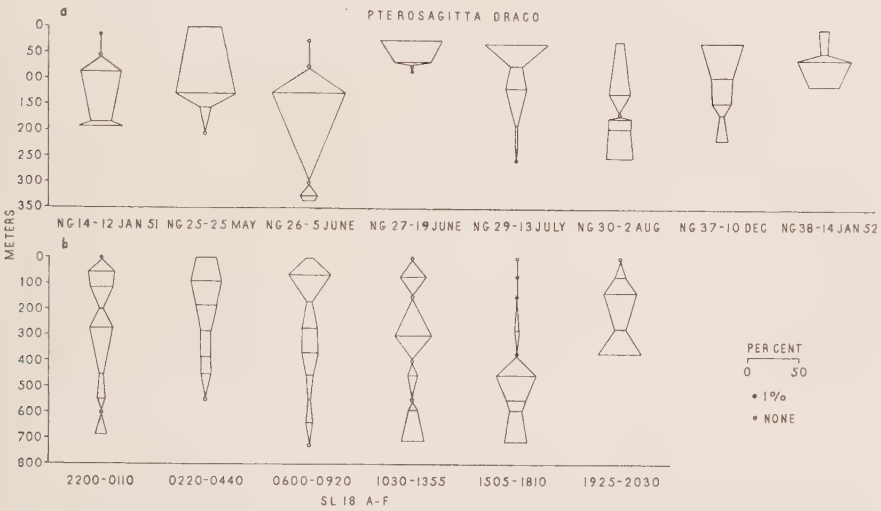

FIGURE 16. *Pterosagitta draco:* a, seasonal variation in vertical distribution at the NG station; b, diurnal vertical distribution at SL 18.

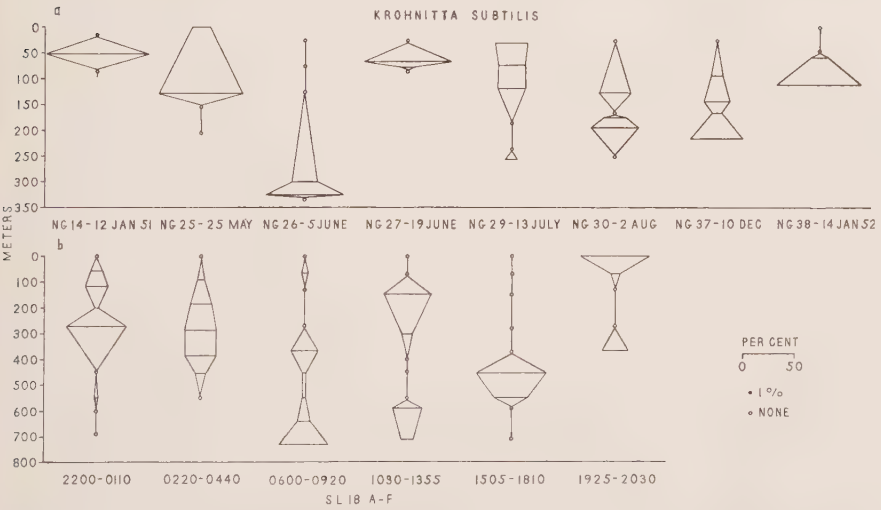

FIGURE 17. *Krohnitta subtilis:* a, seasonal variation in vertical distribution at the NG station; b, diurnal vertical distribution at SL 18.

20-25° C, but at the NG station the mean temperature at the mean day-level was 16.2° C. The known extremes were 7.5 and 24.5° C.

Krohnitta pacifica. Owing to the confusion for many years of this

species with *K. subtilis,* there are almost no data on its vertical distribution. Thomson (1947) found it to be numerous in the upper 240 meters and most abundant between 50 and 100 meters. Tokioka (1951), who took a few specimens in vertical hauls from 10, 50, 150 and 350 meters, found the maximum number at 50 meters. At the NG station it had the shallowest mean day-level and smallest spread of all the species (Table 2). Rare below 200 meters (Figure 18a), it was frequently taken at the surface and in the upper 50 meters. On the other hand, it was found both at the surface and in deep water at the SL station (Figure 18b).

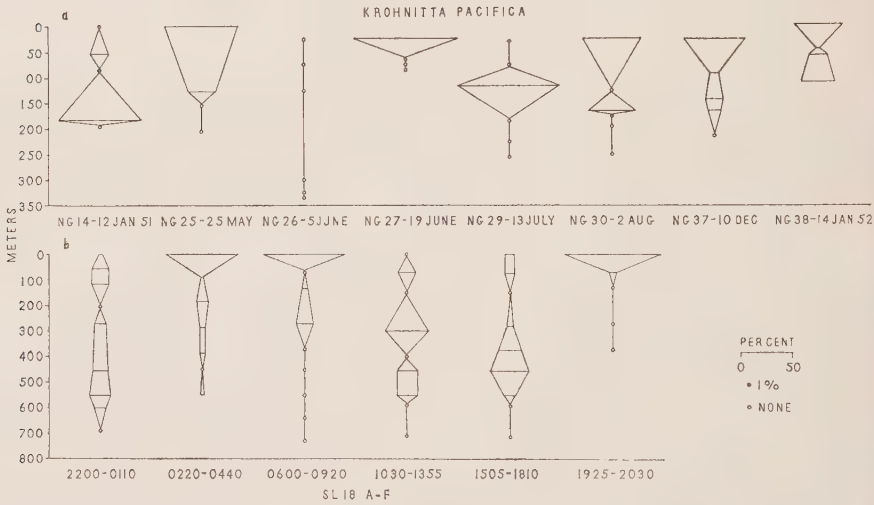

FIGURE 18. *Krohnitta pacifica:* a, seasonal variation in vertical distribution at the NG station; b, diurnal vertical distribution at SL 18.

Concerning diurnal migration, the movement before and around midnight is not clear. Most of the night population in the upper 250 meters appeared to retreat below 250 meters in the daytime. The fact that a large part of the population remained at the surface until late in the morning no doubt indicates a high tolerance for light. Other mainly shallow-water species, *e.g., S. enflata* and *S. serratodentata,* behaved similarly.

Thomson *(op. cit.)* described it as a tropical species, rare in water of 11-19° C and abundant at approximately 20-22° C. A comparison of the numbers collected by Pierce (1951) with his graphs of surface

temperatures shows a total range of approximately 16-29°C. The largest catches in numbers per cubic meter, however, were all taken at 23 and 24° C. The temperature records at the NG station are similar: total range, 17.7-28.3° C; means for the mean 25 to 75 per cent levels, 21.5-25.7° C; mean at the mean day-level, 24.3° C. The lower temperatures recorded for this species at the SL station (Table 5) are closer to the figures reported by Thomson.

Maturity Stages and Breeding Periods

The specimens in the NG subsamples were measured and examined for stage of maturity in an effort to determine the time and extent of breeding periods. Those which were badly damaged or notably shrunken by too strong preservative *(e.g.,* those of NG 7) were not used, but these formed a very small percentage of the total. The material came from thirty series of samples, taken during the months of June through December, 1950, January through August, 1951, October through December, 1951, and January and February, 1952 (NG 1 through 10, 12 through 14, 21 through 31, and 33 through 39; NG 9 and 10, taken in November, 1950, were combined inasmuch as they were separated by only three days and neither was a complete series).

Length. For the study of length-frequency distribution, the total length, that is, the distance from the anterior extremity of the head to the tip of the caudal segment, excluding the caudal fin, was recorded. Those species which may grow to 25 mm or more *(S. enflata, S. hexaptera* and *S. lyra)* were measured to the nearest half millimeter, and the smaller species, to the nearest tenth of a millimeter. For graphing, the lengths of the more abundant species were grouped in 2.0 mm intervals *(S. enflata),* 1.0 mm intervals *(S. bipunctata* and *S. serratodentata)* and 0.5 mm intervals *(S. minima* and *P. draco).* The percentage of individuals in each interval on each date of sampling and the stage(s) of maturity of each group are graphed together. The lengths of the less abundant species *(S. hexaptera, S. lyra, S. hispida, S. helenae, S. decipiens, K. subtilis* and *K. pacifica)* are plotted against the date of sampling.

In the waters off southeastern Australia, Thomson (1947) collected all of the species which occur at the NG station with the exception of *S. hispida* and *S. helenae.* Ranges in length are given, and these,

together with the ranges recorded by Pierce (1951) for species common to the Gulf of Mexico and the Florida Current, are compared with the observed ranges of the Florida Current specimens in Table 6. Thomson's samples came from a large area (24°S to 45°S, 135°E to 154°E); all of the species common to the Florida Current occurred as far south as 38° and some were taken down to 44°S. There is no way to compare directly the temperatures at which the Australian specimens were collected with those at the NG station. However, it is assumed that the greater length attained by most of the species off Australia is associated with lower water temperatures. The maximum size given for the species in the Florida Current generally can be considered the greatest size to which those species grow in tropical waters.

TABLE 6

LENGTH RANGES OF SPECIES FROM THE NG STATION COMPARED WITH RANGES PREVIOUSLY RECORDED.

Species	Range (mm)	Comparison	Numbers[1]
Sagitta enflata	2.5-29.7	Pierce[2], 8-21; Thom[3], 0-5 - 20-25	4132
S. hexaptera	4.3-35.0	Thom, 5-10 - 50-55	84
S. lyra	6.0-32.5	Thom, 0-5 - 45-50	75
S. bipunctata	2.3-13.6	Thom, 2-4 - 16-18	551
S. hispida	3.3-14.0	Pierce, 4.0-13.0	128
S. helenae	3.5-14.5	Pierce, 6.0-15.0	38
S. serratodentata atlantica	2.0-11.5	Thom, 2-4 - 12-14	1851
S. minima	2.6- 7.9	Thom, 2-3 - 8-9	712
S. decipiens	4.0-14.5	Thom, 4-6 - 10-12	157
S. planctonis	13.5	Thom, 5-10 - 30-35	1
Pterosagitta draco	2.9- 8.7	Thom, 2-4 - 10-12	600
Krohnitta subtilis	3.0-13.2	Thom, 6-8 - 12-14	60
K. pacifica	2.3- 7.8	Pierce, 5-7; Thom, 6-7 - 8-9	216
Eukrohnia hamata	9.5-10.0	Thom, 6-8 - 14-16	2

[1]Total numbers measured by the writer.
[2]Pierce (1951). Measurements were made to the nearest millimeter.
[3]Thomson (1947). These are size intervals; exact ranges are not given.

The length of spawning adults of *S. elegans elegans* and *S. elegans arctica* varies widely (Russell, 1932; Kramp, 1917; Dunbar, 1941). As shown in Table 7, size at maturity (stage IV) of other species is also exceedingly variable. In fact, length is a poor indicator of any stage of development, excepting those animals smaller than the approximate lower limit of stage I, which can be presumed juveniles.

TABLE 7

OBSERVED RANGE IN LENGTH (MM) AT EACH OF THE FIVE STAGES OF DEVELOPMENT.

Species	Juvenile	Stage I	Stage II	Stage III	Stage IV
Sagitta enflata	2.5-13.5	6.5-17.0	9.5-20.0	10.0-18.5	11.0-29.7
S. hexaptera	4.3-23.0	13.0-33.0	17.0-31.0	34.0-35.0	27.0
S. lyra	6.0-24.0	17.0-32.5	27.0-30.0	—	—
S. bipunctata	2.3- 8.5	4.5-11.8	8.0-12.4	8.0-12.2	8.5-13.6
S. hispida	3.3- 9.0	6.4-12.0	4.5-14.0	12.8	10.5
S. helenae	3.5- 8.0	6.5-14.5	—	—	—
S. serratodentata	2.0- 8.5	5.0-10.0	5.0-11.0	6.0-10.8	6.0-11.5
S. minima	2.6- 5.4	3.5- 7.9	4.0- 7.5	4.0- 6.5	4.7- 6.5
S. decipiens	4.0-12.5	6.2-13.8	7.2-14.5	8.2-14.5	8.8-12.0
S. planctonis	—	—	13.5	—	—
Pterosagitta draco	2.9- 6.5	4.5- 8.3	5.0- 8.2	5.2- 8.7	5.2- 8.2
Krohnitta subtilis	3.0- 8.0	4.5-13.2	8.5-12.8	12.0-12.5	11.5-13.0
K. pacifica	2.3- 6.1	3.4- 6.2	4.0- 6.5	4.0- 7.8	4.2- 7.0
Eukrohnia hamata	—	9.5	10	—	—

Maturity Stages. There are several methods of dividing the development of Chaetognatha up to maturity into stages, based usually on the relative development of ovaries and testes (Kramp, 1917, 1939; Russell, 1932, 1932a; David, 1955). Thomson (1947), confronted with a large number of species (18), established equivalent stages for all on the basis of the development of ovaries alone. This method was selected for use in the present study. The stages are: juvenile, no development of gonads; I, gonads being formed; II, ova small and all alike in size; III, some ova enlarged to mature size; IV, all ova enlarged.

In indicating stages on length-frequency distribution graphs, the five were reduced to three categories: juvenile, stages I plus II, and stages III plus IV. Clarity was gained and little accuracy lost, since the intermediate category includes all animals with developing but still immature ovaries, and the last category, all those which are fully mature plus those whose ovaries contain some mature eggs and which may be capable of releasing them.

It has been assumed that chaetognaths die after egg-laying (Kuhl, 1938). However, Michael (1911) suggested periodic maturation of the ovaries of *S. enflata* to explain the fact that specimens longer than 20 mm were rarely mature while many under 16 mm had mature ovaries. Thomson (*op. cit.*) suggested that variability in brood lengths might be an explanation, but his sampling method was not suitable

to reveal this, were it so. There is no indication in the NG data that this is the explanation; mature specimens both under and considerably over 16 mm were taken at all seasons. Furnestin (1952) pointed out that *S. enflata* seems to have several sexual cycles in the course of its life. The range in length at maturity of the eight commonest Florida Current species varied from 11 to 63 per cent of the total length range (Table 8). It is likely that several species in addition to *S. enflata* reproduce more than once.

TABLE 8

Length Range at Maturity Expressed as Percentage of Total Length Range.[1]

Species	Percentage
Sagitta enflata	63
S. bipunctata	37
S. serratodentata	48
S. minima	40
S. decipiens	39
Pterosagitta draco	40
Krohnitta subtilis	11
K. pacifica	46

[1]The longest specimens of *S. minima, S. decipiens, P. draco* and *K. pacifica* were found in another stage than IV (Table 7), and the range at maturity of these species is considered to be the difference between the length of the smallest mature specimens and the greatest observed length.

As Dunbar (1941) pointed out, there are indications of a "gradient of breeding habit," the numbers of generations produced per year generally increasing with distance from the poles. In the Arctic, *S. elegans arctica* produces only one brood each year (Dunbar, *op. cit.)* as does *S. gazellae* in the Subantarctic (David, 1955). Farther south, *S. e. elegans* breeds in one long period in the Irish Sea, according to Pierce (1941), but Russell (1932) found four, maybe five, breeding periods in the Plymouth area and Clark *et al.* (1943) concluded that on Georges Bank major spawning occurs in spring and again in late summer or fall. Off the west coast of Florida, three of the five species in inshore waters apparently breed to some extent throughout the year and the other two probably have very long breeding seasons (Pierce, 1951). There is evidence in the NG data that many of the tropical oceanic species off Miami also breed throughout the year.

Individual species. Sagitta enflata. In the diagrams showing percentage length distribution and stage(s) of development (Figure 19), it is

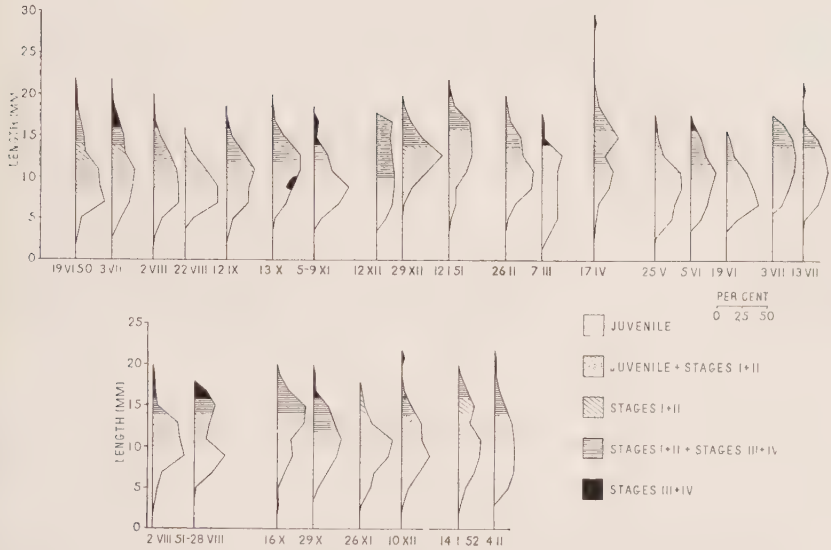

FIGURE 19. Percentage length distribution and stages of development of *Sagitta enflata.*

difficult to recognize separate broods and follow them through to maturity because, in contrast to comparable data for arctic and temperate species, the periods of heavy spawning are superimposed on what appears to be continual spawning throughout the year. The upper size limit of mature individuals decreased from June through August, 1950, and the lower size limit of mature and maturing individuals had decreased by early August and remained the same through the fall, dropping to the lowest observed size on December 12, 1950. This suggests rapid maturation of animals spawned in the warmer months. Possibly the May and June broods reproduced in August and September, and their offspring, in October and November. However, maturation may be much more rapid than this; Russell (1932) believed that *S. elegans* may mature in as few as 43 days during the warmer months. As expected, development was slower during the winter. It appears that the last major spawning of 1950 occurred in late October or early November; four months later, the first indications of heavy spawning in 1951 were found (late February and early March samples). The beginning of the major summer breeding period is apparent in the sample taken May 25, 1951. The lower size limit of reproducing individuals dropped in June, 1951, as it did in early

August, 1950, but instead of remaining at that level, it rose a size interval and leveled off for the rest of the summer and into mid-October. The October 29, 1951, drop to the level of October 13, 1950, could again indicate rapid maturation of a late summer brood.

Although there appears to be more or less continual breeding throughout the year, fluctuations in the relative abundance of juveniles and reproducing individuals should indicate periods of heavy and light spawning. The figures obtained in each month were combined and the monthly percentages of juveniles and of stage III and IV individuals graphed (Figure 20). Juveniles, always more abundant than those in

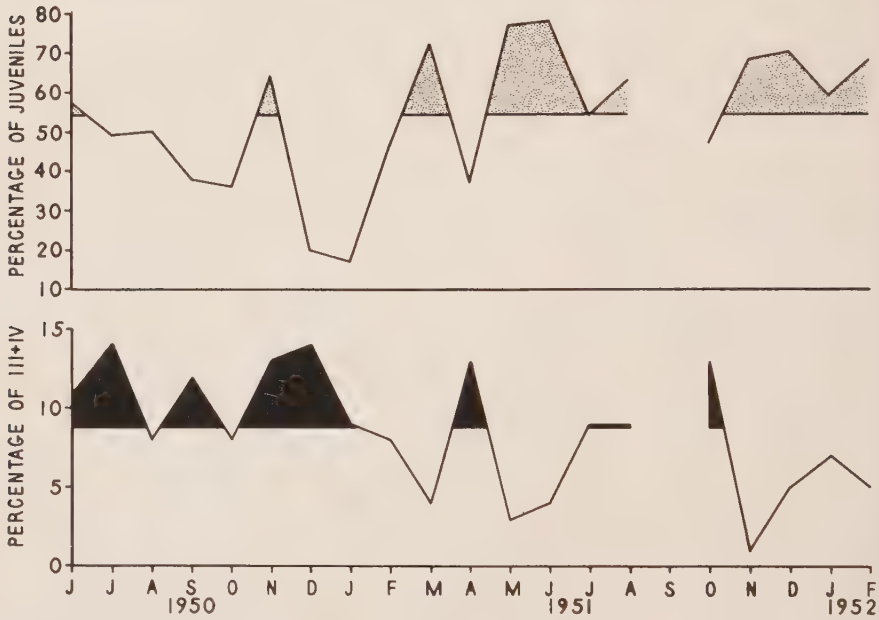

FIGURE 20. Percentage of juveniles compared with percentage of stages III and IV of *Sagitta enflata*. Darkened areas indicate values above the mean percentage.

III and IV combined, comprised from 17 to 78 per cent of the total catch. When the percentage of juveniles rose, that of III and IV dropped, in most months, and a peak of reproducing individuals was usually followed by an increase in the percentage of juveniles in the first to third month thereafter. If the mean percentage of juveniles is chosen as the level at and above which their abundance indicates a period of heavy spawning, then there are three and perhaps four such

periods a year. A spring spawning occurred in March, 1951. The principal reproductive period extended from May through August, with a decline in July of both 1950 and 1951. Fall spawning occurred in November of both years, and in 1951-1952 this continued into the winter months. Since there was a sharp decline in December and January of 1950-1951, it is uncertain whether major winter spawning usually occurs.

The NG records suggest, in agreement with the data of Michael (1911), Thomson (1947) and Furnestin (1952), that the ovaries of this species mature more than once. The animals may mature first when only 11 mm long (Table 7). Spent individuals, measuring from 15 to 20 mm, were collected in January, February, June and July. The largest specimen caught was 29.7 mm long and had fully developed ovaries and testes, the seminal vesicles being distended with sperm.

Sagitta hexaptera. Little information about the breeding of this species was obtained. Only one stage IV (27 mm) and two stage III (34 and 35 mm) individuals were collected, and these in June, July and August. Thomson (1947) found specimens up to 55 mm long but none was fully mature.

Juveniles or stage I individuals or both were taken on each date of sampling, and these together represented 88 per cent of the total catch. The greatest numbers of juveniles appeared in May and July, 1951, and in January and February, 1952; the smallest juveniles were found in May, 1951, and February, 1952 (Figure 21). There is thus some indication that spawning occurs in spring and in fall or winter. Almost no specimens were taken in the summer of 1950, probably because only the upper 25 meters were sampled then (the mean day-level of *S. hexaptera* was 109 M).

Sagitta lyra. No specimens developed beyond stage II were taken; the largest, which was in stage I, measured 32.5 mm. Thomson *(op. cit.)* also found no mature animals, although eight per cent of the largest size category, 45-50 mm, were in stage III. The smallest stage I individuals Thomson found were between 20 and 25 mm, while in the Florida Current a few smaller than 20 mm, the smallest measuring 13.5 mm, were taken. According to the present data, *S. lyra* does not develop to stage II before attaining a length of 25-30 mm. However, Furnestin (1952) reported that some specimens only 15 to 17 mm long were in stage III. Again, repeated production of ova is suggested.

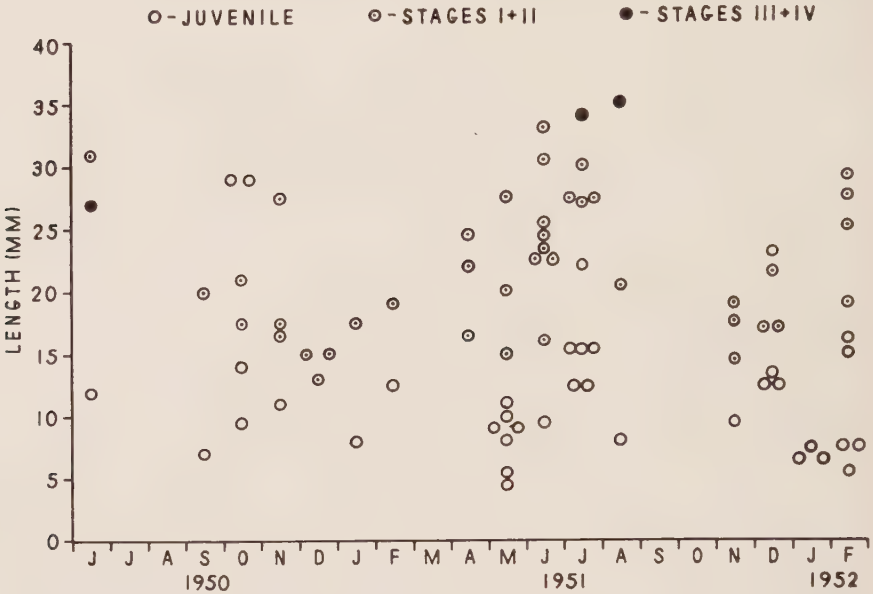

FIGURE 21. Length distribution and stages of development of *Sagitta hexaptera*.

Juveniles under 10 mm in length were taken in May, July, August, September, December, January and February (Figure 22), but without additional data it is impossible to determine if *S. lyra* spawns heavily at certain seasons or breeds throughout the year.

Sagitta bipunctata. Unlike *S. enflata*, this species does not appear to spawn year around, but breeds mainly in early spring or late winter (March 7, 1951; February 4, 1952) and in summer (June, July, 1950; June, August, 1951) (Figure 23). That development of the gonads is slower in the winter months is indicated by the increased upper length limit (8 mm) of the juveniles as a group in winter (December, 1950, 1951; January, 1951, 1952; February, 1952), while in other seasons animals 8 mm long are in stages I or II. No stage III or IV individuals were taken in September and October, 1950, although there were stage I and II specimens which were longer than the mature specimens of late August. If *S. bipunctata* is capable of spawning more than once, the large immature fall specimens may well be summer spawners which are again developing gonads. The appearance of a group of mature individuals about two months later (December 29, 1950) reinforces this hypothesis. The same pattern

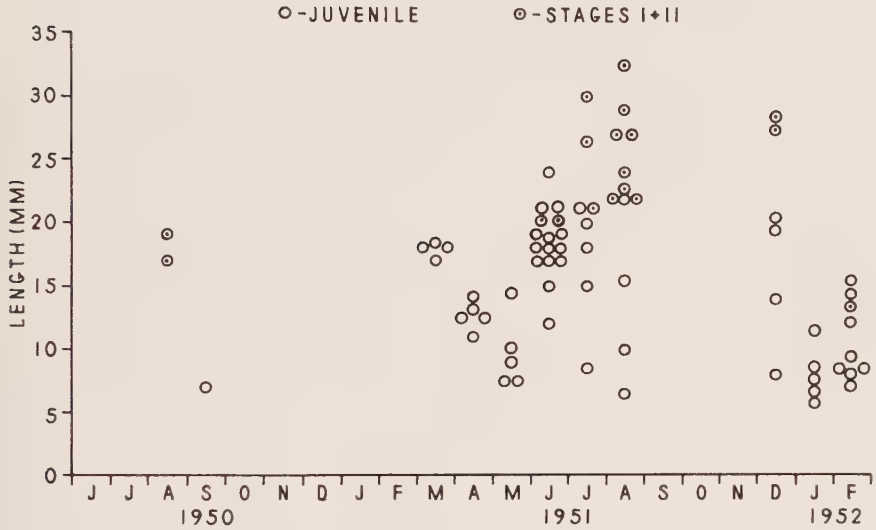

FIGURE 22. Length distribution and stages of development of *Sagitta lyra*.

was not repeated in 1951. However, the numbers of maturing and mature animals had diminished by October 16, and by October 29, those of this size group (10 mm and above) were a mixture of stages I through IV.

Uneven distribution of plankton is probably the best explanation for the absence of mature specimens in February and March, 1951, and the subsequent appearance of newly spawned individuals in March. It will be noted that mature individuals were taken in both January and February, 1952.

Sagitta hispida. In inshore coastal waters where the species is abundant, Pierce (1951) found that it ". . . breeds to some extent the year round . . . . There was no month in which a high percentage of stage I individuals were not present." There were some indications of an increase in reproduction in mid-winter and spring. At the NG station, all specimens except two were juvenile and in stages I and II (the two combined being equivalent to Pierce's stage I) (Figure 24). Major spawning periods may have been responsible for the presence of tiny juveniles (under 5 mm) in spring (April, May, 1951), summer (June, 1951; August, 1950, 1951), fall (November, 1950) and winter (February, 1952).

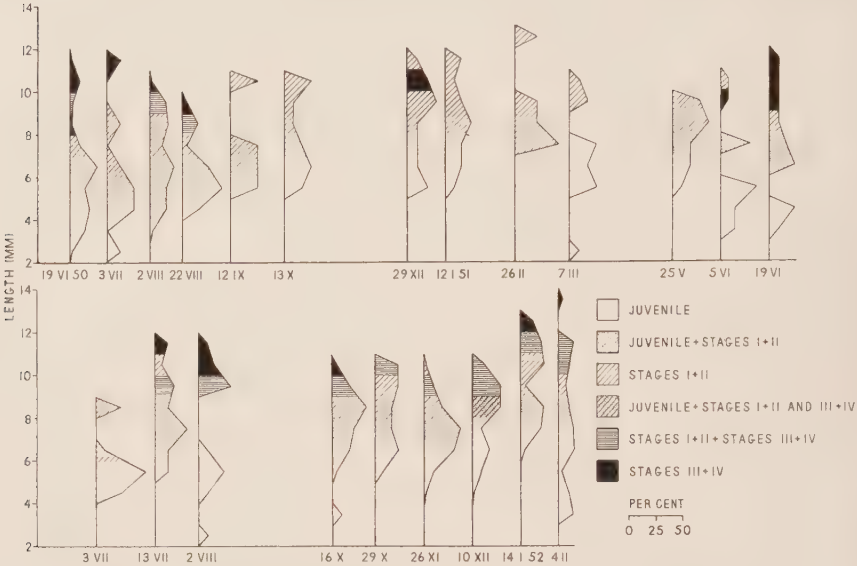

FIGURE 23. Percentage length distribution and stages of development of *Sagitta bipunctata.*

Size at maturity ranges from 5 to 12 mm and individuals mature at 8 mm are common, according to Pierce. Only two mature specimens, 10.5 and 12.8 mm, were taken at the NG station.

Sagitta helenae. Pierce *(op. cit.)* found that it breeds year around, perhaps accelerating its reproductive rate in May and June. It was most abundant at the NG station on April 9, 1951, and most of the specimens were juveniles, ranging from 3.5 to 8.0 mm (Figure 25). Thus spring spawning is definitely indicated. No mature animals were found.

Sagitta serratodentata. This common species, like *S. enflata,* appears to breed throughout the year (Figure 26). Although the December 29, 1950, and January, 1951, samples indicate a reduction in reproductive rate, this was not repeated in December and January of the following winter. Above average monthly percentages of juveniles in October of both years and in February through May suggest that the major breeding periods occur in fall and spring (Figure 27). The sustained high percentage of juveniles in the winter of 1951-1952 may have been an early manifestation of the spring spawning period. Percentages of mature individuals were above the mean either during or preceding the above average percentages of juveniles. The great increase in per-

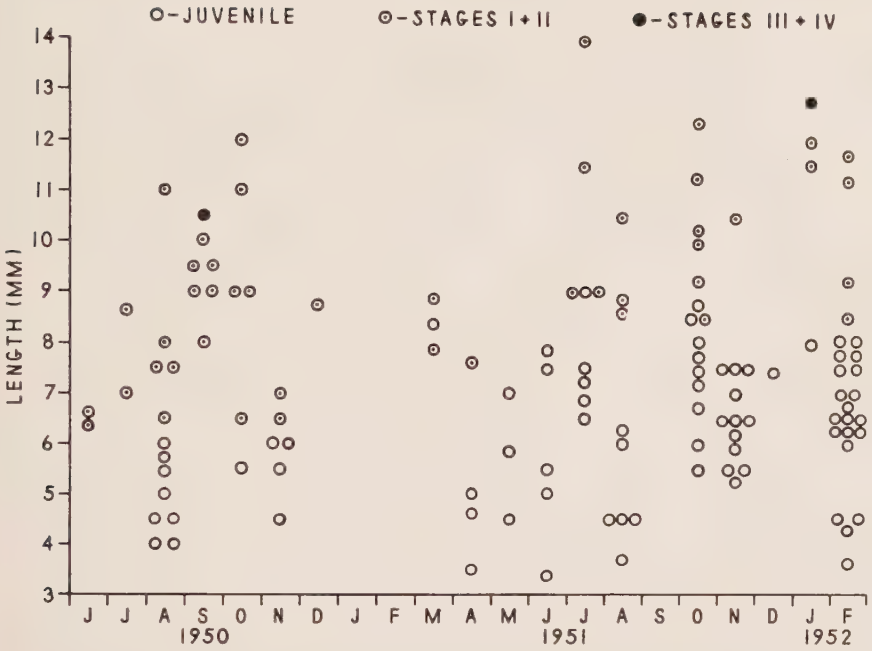

FIGURE 24. Length distribution and stages of development of *Sagitta hispida*.

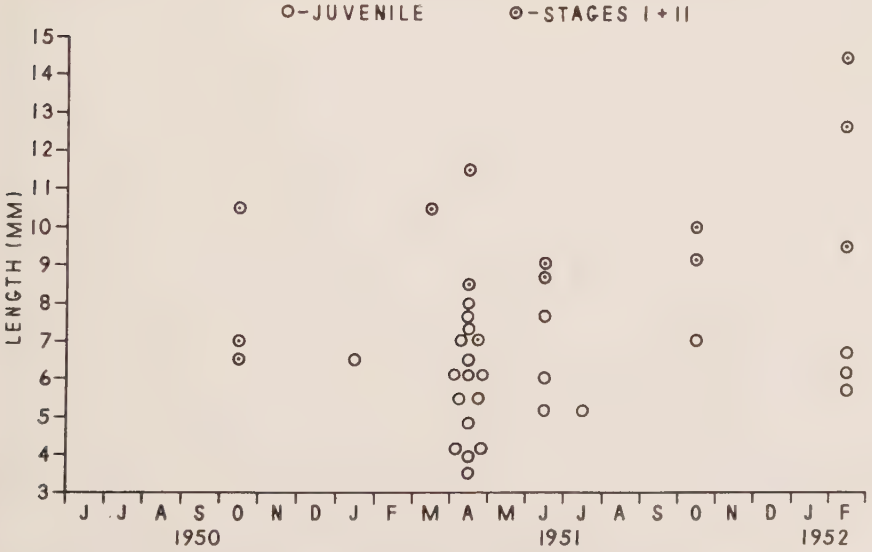

FIGURE 25. Length distribution and stages of development of *Sagitta helenae*.

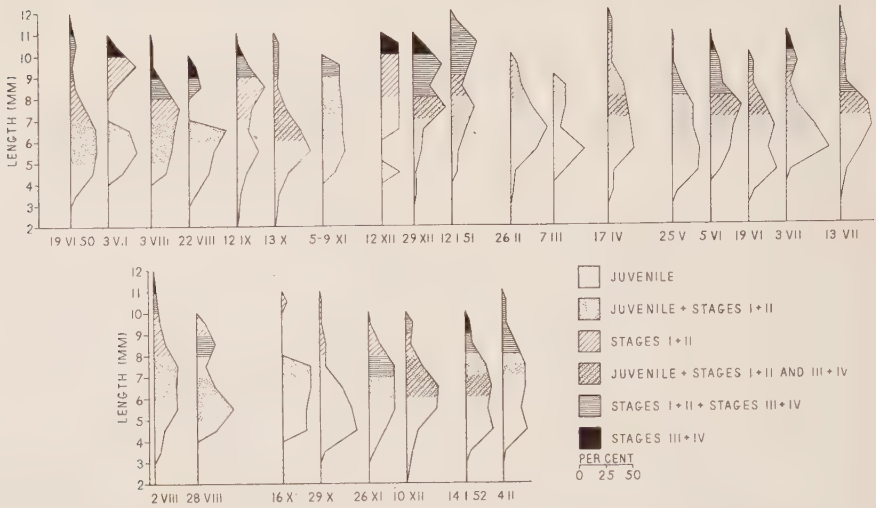

FIGURE 26. Percentage length distribution and stages of development of *Sagitta serratodentata*

centage of mature specimens in the winter preceding the 1951 spring acceleration in reproduction is especially striking.

Ova may mature when the animal is as small as 6 mm long (Table 7); specimens ripe at 7 mm are not uncommon. The fact that groups of immature individuals (juvenile, I and II) measuring 9 mm and longer were taken in all months of the year except January and May indicates that this species is capable of reproducing more than once.

Observations have not confirmed the statement of Thomson (1947) that *S. serratodentata* is markedly protandric, at least during all of its life. It was not at all unusual to find specimens from 6.5 to 8.5 mm long with ovaries in stage III or IV and with either no development of the male organs or with the seminal vesicles just beginning to appear. Conversely, within the same size range, specimens with the ovaries in stage I, the testes in varying stages of development and the seminal vesicles fully formed were found. A number of these, from 6.5 to 8.2 mm, had been fertilized, for the seminal receptacles, enlarged with spermatozoa, could be seen clearly. By the time the animals are approximately 8.5 mm long, the male organs are usually well developed while the ovaries may be in any stage from I to IV. Examples are specimens at 8.5 mm in stage II, 9.5 mm in IV, 9.7 mm in I, and 10.0 mm in I, II or IV, and all with spermatocytes and spermatozoa filling

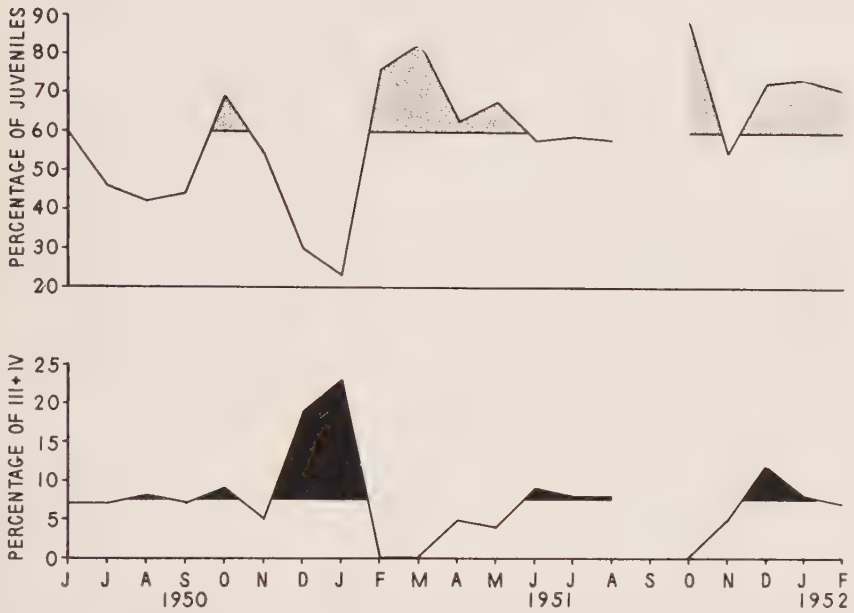

FIGURE 27. Percentage of juveniles compared with percentage of stages III and IV of *Sagitta serratodentata*. Darkened areas indicate values above the mean percentage.

the caudal coelom and with fully formed seminal vesicles, often turgid with spermatozoa. It is unlikely that individual variation in the time of development of one set of gonads relative to the other ranges all the way from protogyny to protandry. The most reasonable explanation seems to be that the female organs begin development first, the ova maturing rapidly, so that an animal may bear ripe ova by 6.0-6.5 mm. Probably the ovaries first mature when the animal is approximately 6-7 mm long. Observations indicate that the seminal vesicles begin development before the testes, appearing first as a pair of epidermal thickenings between the posterior lateral and the caudal fins when the animals are approximately 6-8 mm long. Thus it can be assumed that specimens of 6.5-8.2 mm, with ovaries in stage I, the receptacles filled with sperm and the vesicles well developed, have already shed fertilized ova. Spermatozoa have been produced by the time the animals reach a length of 8 mm or so. Meanwhile ova are again being produced. Doubtless the examination of these larger specimens in which the male gonads are nearly or fully mature while the female gonads

are still immature has led to the conclusion that *S. serratodentata* is protandrous.

Sagitta minima. Spawning periods on a year-around basis are difficult to discern because *S. minima* was particularly uncommon in the September, 1950, and the November, 1950, through April, 1951, samples (Figure 28). During the latter period, no juveniles were taken. However, the presence of groups of small juveniles in January and February, 1952, shows that winter spawning may occur. The principal breeding period comes in the summer months, probably beginning in May. Also there is evidence of fall spawning (October, 1950; November, 1951).

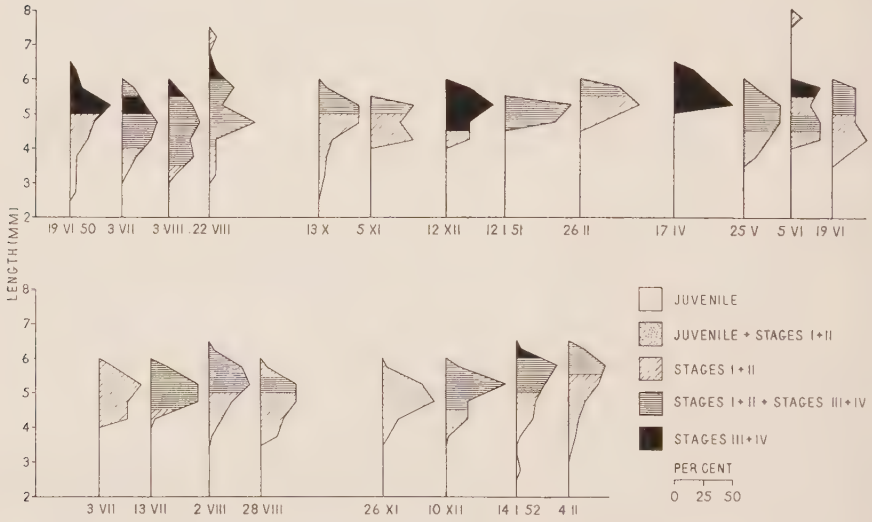

FIGURE 28. Percentage length distribution and stages of development of *Sagitta minima.*

Although Thomson (1947) found no stage IV specimens smaller than 7 mm, specimens of 5 mm and less with mature ovaries were commonly found in the Florida Current. The smallest measured 4.6 mm. It is notable that specimens of 7 mm and longer were rarely taken, while Furnestin (1952) reported a length range of 7.5 to 10.0 mm and Thomson, up to 9.0 mm. Some evidence of repeated maturation of the ovaries is seen in the samples of July 3 and August 22, 1950, and June 5 and August 28, 1951, when there were immature

individuals longer than the mature ones. Presumably the ovaries may first ripen when the animal is approximately 5-6 mm long, and then a subsequent maturation may occur.

Sagitta decipiens. Mature individuals were not found except in June, August and December, which may mean that spawning occurs only in summer and winter. If this is so, a breeding pattern can be hypothesized from the distribution of length and stage of development (Figure 29), as follows. Specimens spawned in May or June and appearing in

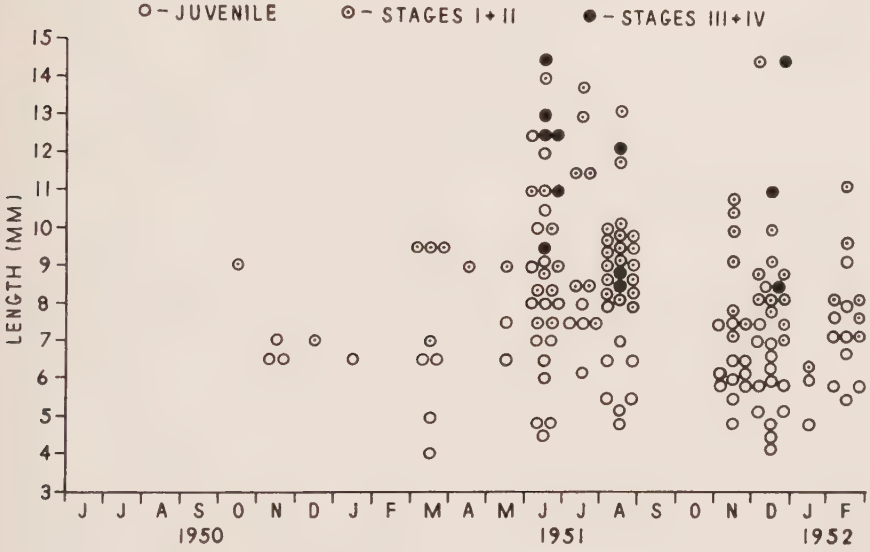

FIGURE 29. Length distribution and stages of development of *Sagitta decipiens.*

June as juveniles of 4-5 mm reach maturity at 8-9 mm in August and spawn. This late summer brood matures more slowly than that of early summer but is 8-9 mm long and breeding in December, at the same time as the early summer brood, now 11 mm or more in length, is breeding again. The range of length at maturity and the considerable overlap in range of all the developmental categories (Table 7) suggest that the ovaries do mature more than once. Perhaps the early summer brood dies after this second spawning, or a few survive the winter and are represented by the large (14 and 14.5 mm) specimens taken in June, 1951. More likely, these large individuals are remnants of the late summer brood which spawn in June for the second time. The

December brood matures even more slowly than the late summer brood, and these are the smallest mature animals found in June and breeding then for the first time. Probably they are able to breed again in August. Thus, theoretically, each brood is derived from at least two earlier broods, lives from six to ten months to a year, and spawns twice if not more often. On the other hand, the presence of juveniles of 7 mm and less in all months except April, September and October (Figure 29) may reflect a general year-round spawning farther out at sea.

Furnestin (1952) did not find any specimens with completely mature seminal vesicles, but she noted that, contrary to the statement of Ritter-Záhony, the vesicles never touch the posterior fins or the caudal fin. Instead, she observed, there is sometimes a swelling of the caudal segment which gives the illusion of a union between vesicle and caudal fin. In the Florida Current material, two specimens with fully formed seminal vesicles were found, and although the vesicles were separated from the posterior fins, they definitely did extend to the caudal fin. No swelling of the caudal segment was observed.

Pterosagitta draco. Since a fairly large stock of juveniles was present in most months (Figure 30), it can be assumed that spawning occurs throughout the year. The monthly percentage of juveniles rose above the mean in October, 1950 and 1951, in February, April and May, 1951, in August, 1950, and in July, 1951, indicating that spawning had been especially heavy during these periods (Figure 31).

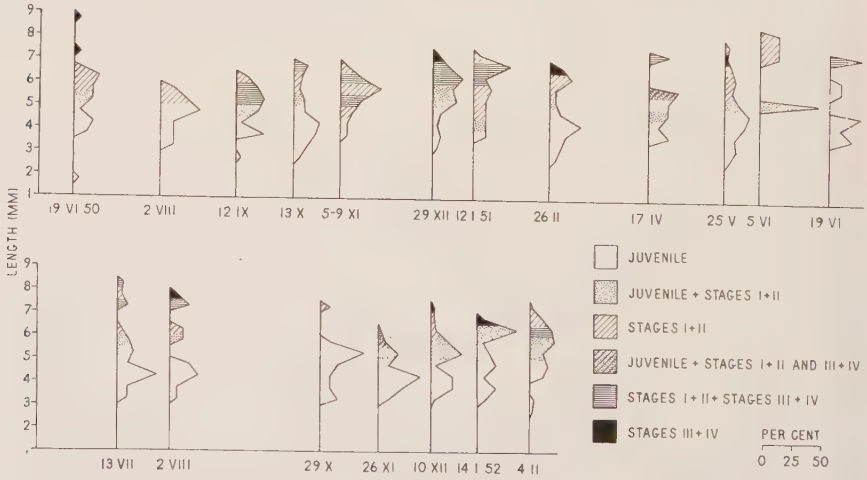

FIGURE 30. Percentage length distribution and stages of development of *Pterosagitta draco.*

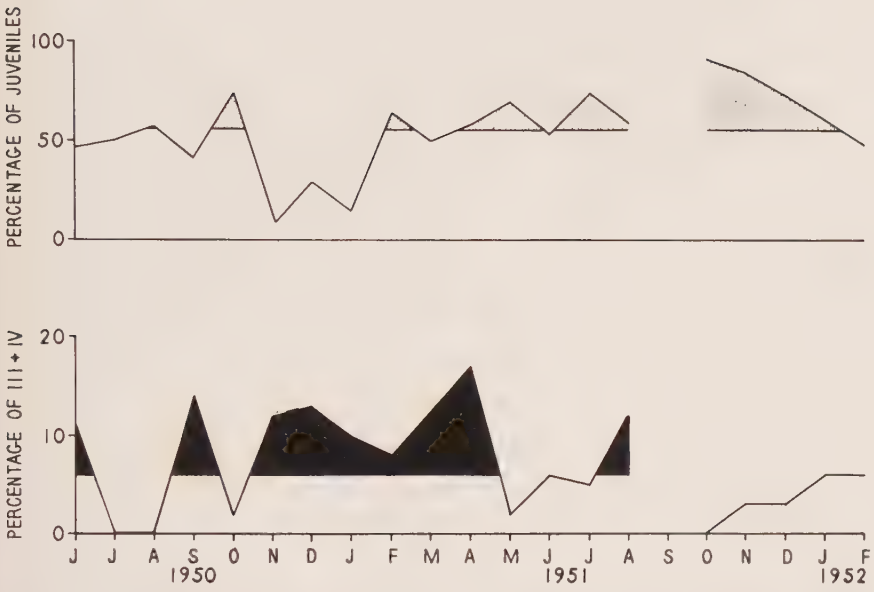

FIGURE 31. Percentage of juveniles compared with percentage of stages III and IV of *Pterosagitta draco*. Darkened areas indicate values above the mean percentage.

Probably individuals may spawn more than once. The overlap in length range of all stages of development, the wide range in length of mature specimens (Table 7), and the frequent presence of a group of stage I and II individuals longer than the mature specimens all indicate this.

Observations have suggested that *P. draco* may not be invariably protandrous. Between 5 and 6 mm, the ovaries may be in stage IV, the testes not apparent, and the seminal vesicles just beginning to show as epidermal thickenings. Alternatively, the ovaries may be in stage I or II and the testes and seminal vesicles fully developed, but this condition is relatively unusual. The male organs are usually not formed until the animal is at least 6.5 mm long. Past 7 mm, specimens are frequently found in which the ovaries are in stage I or II, the seminal receptacles distended with sperm, the caudal segment clear of male products and the seminal vesicles either not apparent or else atrophying. Presumably these animals have released spawn and their ovaries are again beginning development. As in the case of *S. serratodentata,* there is thus some evidence that female maturity may be

reached when the animal is quite small and before the development of male organs has begun.

Krohnitta subtilis. The small amount of data available does not give evidence of continuous breeding. Mature specimens were found only in summer (Figure 32). Spawning must also occur in winter, for juveniles less than 5 mm long appeared in the February and December, 1951, and in the February, 1952, samples.

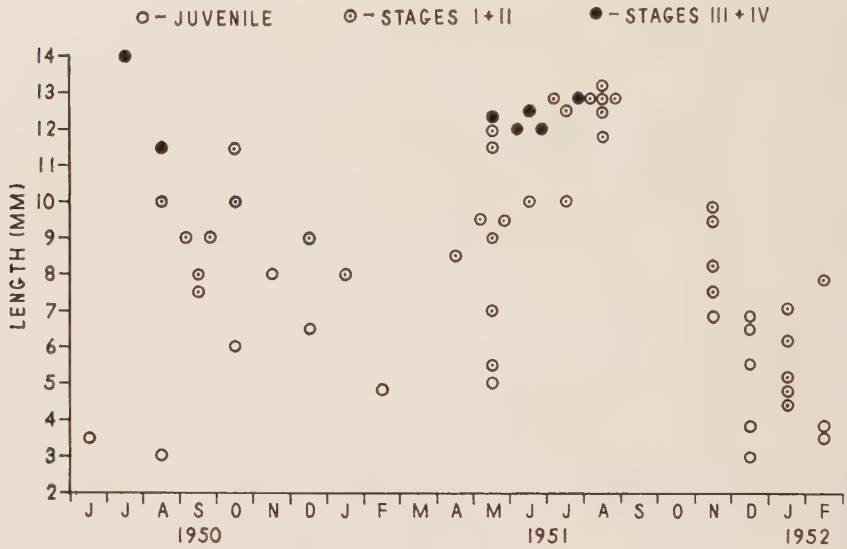

FIGURE 32. Length distribution and stages of development of *Krohnitta subtilis.*

The observed range in length at maturity expressed as percentage of the total length range is the lowest of all the commoner Florida Current species (Table 8). No mature specimens shorter than 11.5 mm were found. On the other hand, development of the gonads may begin when the animal is as short as 4.5 mm or as long as 13.2 mm (Figure 32). One may assume that in the larger stage I and II specimens the gonads are developing after an earlier period of maturation, but additional data are required to establish this.

Krohnitta pacifica. Pierce (1951) noted that whenever this species was abundant, invariably some of the specimens were mature, suggesting that the breeding season in this region is long. In the Florida

Current, mature individuals appeared during almost every month in which samples were taken (Figure 33). Comparatively, juveniles were quite rare; most of them measured under 4 mm, and no doubt most of those taken were lost in or through the net. Probably *K. pacifica* breeds throughout the year. The abundance of mature specimens in the summer of 1950 (although not in 1951) and in the winter of 1952 (although not in 1951) indicates that the major spawning periods may occur in summer and winter.

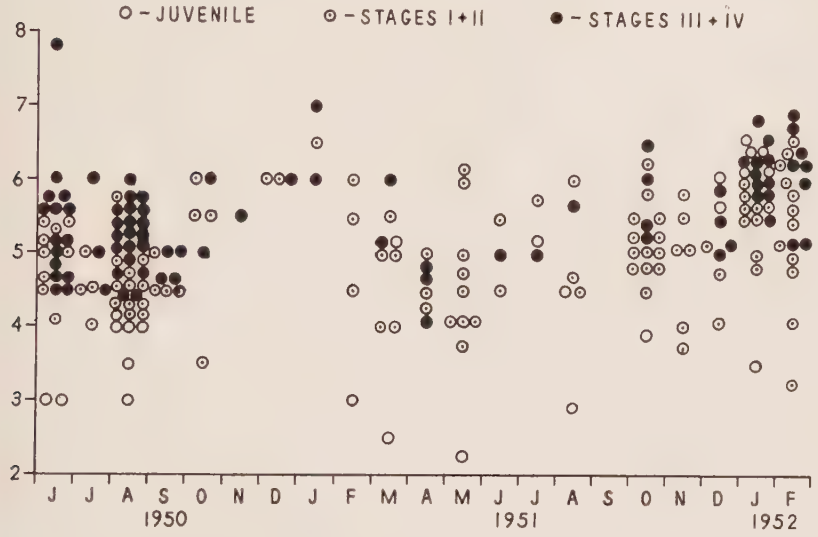

FIGURE 33. Length distribution and stages of development of *Krohnitta pacifica*.

Mature specimens of 4.2 to 6.0 mm were common, although animals in all stages of development were found in this size category. Thomson (1947) apparently took none smaller than 6.0 mm, and none of those measuring 6.0 to 7.0 mm had developed beyond stage II. The specimens collected by Pierce *(op. cit.)* were 5.0 to 7.0 mm long, and among them were many mature animals, although the published records do not show the distribution of stages at the various lengths. In any case, development is obviously faster in the warmer waters of the Florida Current and the coastal Gulf of Mexico than in the waters off southeastern Australia, investigated by Thomson.

The overlap of the length ranges of the several developmental stages (Table 7) indicates repeated maturation of the ovaries.

Discussion

The usual assumption that there is slight annual variation in tropical oceanic conditions (*e.g.*, Smith *et al.*, 1950) was in general confirmed by hydrographic observations at the NG station (Miller *et al.*, 1953). Seasonal changes in temperature and the concentration of nutrient salts were obscured by water mass changes. Under these conditions one would expect that there might not be much annual fluctuation in the abundance of animals. However, most chaetognath species had distinct periods of maximum abundance. These periods may relate, partly at least, to water-mass changes as in Bermuda (Moore, 1949; Hela *et al.*, 1953), although no definite indicators of either the Gulf of Mexico or the Yucatan components of the Florida Current were found. The one possible indicator of Gulf water is significant not in presence or absence but in relative abundance, which is thought to depend on its spawning periods in the Gulf, on circulation in the eastern Gulf and, of course, on the amount of Gulf water entering the Florida Current. On the other hand, the periods of maximum abundance of several species *(Sagitta enflata, S. bipunctata, S. helenae, S. serratodentata, S. minima, Krohnitta subtilis* and *K. pacifica)* coincided generally with their main breeding periods; water-mass changes did not appear to mask seasonal changes at all.

However, differences in the fauna of the eastern and western portions of the Current suggest differences in the components of the two parts. Comparison of the chaetognath fauna at the NG station with that in an area about thirty miles to the east (SL station) showed slight differences in species composition and marked differences in relative abundance and vertical distribution. *Sagitta helenae* and *Eukrohnia hamata* were not taken at the SL station, and *E. fowleri* did not occur at the NG station. The species of *Eukrohnia* apparently differ in their temperature requirements, and their distribution relative to observed temperatures at the two stations has been discussed in the section on abundance. The absence of *S. helenae* at the SL station is not significant; strays probably occur there, since the species has been taken as far east as Bermuda (Moore, *op. cit.).*

The physico-chemical characteristics of the Florida Current at the NG station are oceanic and there is no evidence that east coast inshore waters contribute to it at all (Miller *et al., op. cit.).* In this area, the Current flows over the edge of the continental shelf. The nature of the chaetognath fauna definitely suggests that factors arising from this physical situation or from the contribution to the Current of coastal

TABLE 9

LIST OF SAMPLES TAKEN AT THE NG STATION.

Sample Number	Date	Time	Depth (meters)	Wet Volume (cc)	Towing Distance (mi.); Remarks
1	19 June '50	2200	0-25	14	Towing distance unknown
2	3 July '50	2200	0-25	11	" " "
3	2 Aug. '50	1030	27	28	" " "
4A	3 Aug. '50	1015	75	3	" " "
4B		1050	25	9	" " "
4C		1128	175	8	" " "
4D		1215	125	10	" " "
4E		1254	250	5	" " "
5A	22 Aug. '50	1030	16	3	" " "
5B		1140	96	7	" " "
6A	12 Sept. '50	1108	33	7	" " "
6B		1151	90	28	" " "
7	3 Oct. '50	0930	12	11	" " "
8A	13 Oct. '50	0910	32	10	" " "
8B		0947	25-75	32	" " "
8C		1030	75-125	5	" " "
8D		1140	115-150	8	" " "
9A	5 Nov. '50	1400	50	7	" " "
9B		1424	surface	2	" " "
10A	9 Nov. '50	1230	100-230	1	
10B		1250	surface	4	for 10A, B, C & D; net
10C		2345	130-170	0.5	fouled in 10 A, C & D
10D		2345	110-130	2	
12	12 Dec. '50	1030	0-100	10	One-half hour diagonal haul; distance unknown.
13A	29 Dec. '50	1420	50-90	7	Towing distance unknown
13B		1525	0-40	38	" " "
14A[1]	12 Jan. '51	1106	0-10	<1	2.0
14B		1157	9-27	<1	2.0
14C		1242	40-64	14	1.6
14D		?	82-91	10	1.5
14E		1416	192	18	0.95
14G		1550	182	3	0.8
16[1]	28-30 Jan. '51		0-238		24-hour Station
21A	26 Feb. '51	1230	0-92	22	1.6
21B		1310	110	5	0.45
22A	7 Mar. '51	1100	surface	5	Towing distance unknown
22B		1130	5-50	5	" " "
22C		1215	180	10	" " "
23	9 Apr. '51	1330	surface	15	" " "
24C	17 Apr. '51	1245	100	6	" " "
24D		1320	200	15	" " "
24E		1417	150	8	" " "
24F		1455	surface	21	" " "

[1]Series used in vertical distribution studies.

TABLE 9, Continued

LIST OF SAMPLES TAKEN AT THE NG STATION.

Sample Number	Date	Time	Depth (meters)	Wet Volume (cc)	Towing Distance (mi.); Remarks
25A[1]	25 May '51	1105	surface	25	Towing distance unknown
25B		1145	surface	10.5	0.45
25C		1220	119-138	16	0.50
25D		1300	146-165	21	0.85
25E		1340	283	13	Towing distance unknown
25F		1420	183-229	4	1.0
26A[1]	5 June '51	1020	0-50	1	1.0
26B		1110	50-100	<1	0.9
26C		1110	100-150	7	0.9
26D		1240	280-320	2	0.6
26E		1240	320-350	3	0.6
26F		1320	300-350	5	1.1
27B	19 June '51	1128	0-45	14	1.15
27C		1205	55-75	9	0.90
27D		1240	70-100	1	1.15
27E		1330	70-85	<1	1.05
28A	3 July '51	0925	0-80	27	1.70
28B		1015	65-135	?	Sample lost
28C		1015	135-210	7	0.7
28D&E[2]					
29A[1]	13 July '51	0900	0-60	39	2.0
29B		0955	50-95	3	0.5
29C		0955	95-140	6	0.5
29D		1040	165-210	2	0.85
29E		1040	210-255	2	0.85
29F		1140	210-300	3	0.85
30A[1]	2 Aug. '51	0945	0-50	12	1.5
30B		1135	105-145	3	0.6
30C		1135	145-185	9	0.6
30D		1150	160-185	5	1.2
30E		1150	185-200	5	1.2
30F		1350	225-275	20	1.5
31	7 Aug. '51	1107	surface	11	1.2
32-1	28 Aug. '51	1100	55	9	0.9
32-2		1100	115	7	0.9
32-3		1235	151	1.5	0.7
32-4		1235	185	4	0.7
32-5		1140	167	5	0.6
32-6		1140	242	4	0.6
33	28 Aug. '51	1315	0-219	20	Towing distance unknown; diagonal haul
34	16 Oct. '51	1000	0-100	63	Towing distance unknown; diagonal haul

[1]Series used in vertical distribution studies.
[2]No data.

TABLE 9, Continued

List of Samples Taken at the NG Station.

Sample Number	Date	Time	Depth (meters)	Wet Volume (cc)	Towing Distance (mi.); Remarks
35A	29 Oct. '51	0903	surface	24	2.0
35B	29 Oct. '51	0903	37	27	2.0
36A	26 Nov. '51	1025	37	15	1.5
36B		1025	20-60	3	Towing distance unknown; depth estimated
36C		1111	60-100	2	"
36D		1111	110-133	5	"
36E		1205	140-160	9	"
37A[1]	10 Dec. '51	1136	9-46	22	2.0
37B		1310	69-115	2	0.45
37C		1310	119-165	4	0.45
37D		1400	151-179	3	1.1
37E		1400	201-229	5	1.1
38A[1]	14 Jan. '52	1010	surface	47	1.7
38B		1055	59	3	0.3
38C		1055	110	11	0.3
38D		1145	110	11	0.3
38F		1248	46	9	1.1
39A	4 Feb. '52	1015	surface	20	3.1
39B		1105	50	13	1.2
39D		1153	96	15	2.1
39E		1153	146	8	2.1
39F		1240	96	37	2.4
39G		1240	146	13	2.4

[1]Series used in vertical distribution studies.

waters from Caribbean islands or the Gulf of Mexico or both produce a mixed neritic and oceanic population. The species which seem to associate in particular with waters over the edge of the continental shelf, *S. enflata* and *S. minima,* and the neritic species *S. hispida* and *S. helenae* were relatively much more abundant at the NG than at the SL station, while most of the oceanic species *(S. hexaptera, S. lyra, S. serratodentata, S. decipiens, P. draco, K. subtilis* and *K. pacifica)* were commoner at the SL station. Assuming that the SL data generally show the relative abundance of species there, this part of the Current resembles the area sampled off North Carolina by Bumpus and Pierce (1955) more than that at the NG station since the neritic aspect is virtually absent in the other two localities. It is suggested, therefore, that the waters which contribute neritic species to the Current off

Miami are confined to the western part and that their characteristic fauna does not long survive oceanic conditions.

Vertical Distribution. The relationship between the west-to-east downward slope of the isotherms across the Current and the fact that the 50 per cent levels of all species at the SL station were much deeper than the mean day-levels of the same species at the NG station was discussed in the section on vertical distribution. Probably differences in the depths of the isotherms are responsible for the gross differences in the levels occupied by chaetognaths. A study of the effects of temperature and light on the midday vertical distribution of certain species of pteropods, siphonophores, chaetognaths and copepods at the NG station showed that as the level of the 15° C isotherm became shallower, the mean day-levels tended to become shallower (Moore *et al.*, 1953). Although the correlation between mean day-level deviations and deviations in the depth of the 10^{-2} isolume was not significant, the value was large enough to suggest a possible relation. An analysis of the relationship between the spread of the Chaetognatha as a group and the deviations of the levels of the 15° C isotherm and the 10^{-2} isolume showed that the response to temperature increases and the response to light decreases markedly from the 25 to the 75 per cent level. This suggests that the level of the upper part of the spread of chaetognaths is controlled predominantly by light and that temperature predominantly controls the lower levels.

Moore (1949) found a significant increase in spread in the deeper-living species at Bermuda, all groups being combined. The same was true at the NG station (Moore *et al., op. cit.*). Positive correlations were also found between the mean day-levels and mean spreads of the separate groups, although only that for the copepods was significant. As a generalization, this relationship between spread and depth does not always apply to individual species. The deep-living *S. lyra* had a lesser spread than many of the so-called epiplanktonic species at the NG station, and at the SL station its spread was the smallest of all (Table 2). The data suggest that the vertical distribution of *S. lyra* is controlled predominantly by temperature. Conversely, *S. decipiens,* another deep-living species, had the most extensive spread of all at the NG station and next to the largest at the SL station.

The relationships, so far as they could be ascertained, of the depths of the 25 to 75 per cent levels and the degree of spread of the individual species to temperature in particular and to light in general have been discussed in the section on vertical distribution. The effect of

illumination on the depths of the major concentrations of the various species is difficult to assess. Obviously, the intensity of light is much greater at the NG mean day-levels than at the 50 per cent levels of most of the same species at the SL station. This and the fact that there was no significant correlation between mean day-level deviations and deviations in the depth of the 10^{-2} isolume suggest that chaetognaths have a wide range of tolerance for light.

Vertical distribution of species at the NG station was highly variable seasonally. It has sometimes been assumed that the younger stages of planktonic animals occupy shallower levels than the older ones. David (1955) found that the size of *S. gazellae,* which does not migrate diurnally, increases with depth, and Russell (1931), that the younger *S. elegans* are the first to migrate to the surface at dusk and the last to leave in the morning, thus appearing to withstand higher light intensities than the older animals. In the Florida Current, no especial concentrations of small juveniles were found in the upper layers even at times when spawning appeared to have been heavy. For example, on June 5, 1951, small *S. enflata* were taken both between 100 and 150 meters and between 300 and 350 meters, and comparatively few occurred in the upper 50 meters. This is in accordance with the suggestion of Gunnar Thorson (personal communication) that the conditions of temperature and perhaps other factors into which a planktonic animal hatches generally prescribe its range as an adult. Marshall and Orr (1955), summarizing results of experiments on the lethal temperatures of groups of *Calanus finmarchicus* spawned at different seasons and of northern and southern races of cladocerans, have already suggested that the temperature conditions in which the animals have developed may define their ability to withstand temperature changes. Each of the 11 commoner species at the NG station ranged from the surface to 350 meters, except *K. pacifica* (0-292 M). It is almost impossible to believe that all the members of a population of *S. enflata,* for example, are able to tolerate the observed range of 7.9-27.6° C. However, the idea that small juveniles found in deep water have been spawned there and will spend the remainder of their lives there, moving vertically and horizontally within the bounds of their tolerances to physicochemical changes encountered, and that there may be similarly circumscribed intermediate and shallow-water groups within the species is quite plausible. Changes in level would be expected as changes in the levels of isolumes and isotherms, whether seasonal or water-mass or both, occur.

TABLE 10
LIST OF SAMPLES TAKEN AT THE 24-HOUR STATION SL 18 ON JUNE 30-JULY 1, 1953.

SAMPLE NUMBER	TIME	DEPTH (meters)	CORRECTION FACTOR[1]
A-0	2200	0	2.1
A-1	"	58.5	"
A-2	"	118.8	"
A-3	2255	202.9	3.3
A-4	"	274.2	"
A-5	2405	457.0	3.7
A-6	"	548.4	"
A-7	0110	601.4	3.1
A-8	"	685.5	"
B-0	0220	0	1.3
B-1	"	91.4	"
B-2	"	182.8	"
B-3	0330	285.2	3.9
B-4	"	383.9	"
B-5	0440	457.0	2.6
B-6	"	548.4	"
C-0	0600	0	1.9
C-1	"	67.6	"
C-2	"	137.1	"
C-3	0710	274.2	6.2
C-4	"	365.6	"
C-5	0815	457.0	2.8
C-6	"	548.4	"
C-7	0920	639.8	3.1
C-8	"	731.2	"
D-0	1030	0	1.3
D-1	"	73.1	"
D-2	"	146.2	"
D-3	1125	301.6	2.2
D-4	"	402.2	"
D-5	1235	457.0	3.1
D-6	"	548.4	"
D-7	1355	590.4	2.4
D-8	"	712.9	"
E-0	1505	0	1.3
E-1	"	76.8	"
E-2	"	155.4	"
E-3	1555	279.7	1.6
E-4	"	374.7	"
E-5	1705	457.0	3.4
E-6	"	548.4	"
E-7	1810	590.4	2.8
E-8	"	712.9	"
F-0	2030	0	no data
F-1	"	67.6	" "
F-2	"	137.1	" "
F-3	1925	274.2	" "
F-4	"	365.6	" "

[1]For converting numbers per sample to numbers per mile.

Diurnal Migration. Bumpus and Pierce (1955) found no consistent evidence of diurnal migration in their samples taken off North Carolina except in one species, *S. minima,* which appeared to be more abundant in the deeper samples. No mention was made of the time of day when the samples were taken. Of the six fairly-abundant-to-common oceanic species at Bermuda, three exhibited slight, and three, definite diurnal migration (Moore, 1949). All of these species were taken by Bumpus and Pierce (*op. cit.*). In the single 24-hour series of samples from the SL station, diurnal migration of most of the species showed clearly. Definite migrants were *S. enflata, S. hexaptera, S. lyra, S. serratodentata, P. draco* and *K. pacifica.* There is some evidence that *S. decipiens* and *K. subtilis* were migrating. There were too few specimens of *S. minima, S. hispida, S. helenae* and *S. bipunctata* to show vertical movement, but Moore (*op. cit.*) found that the last species does migrate diurnally.

Variations in the general pattern of movement toward the surface with diminishing light and away with increasing light were found. A tendency toward continuing downward movement in the afternoon was seen in the "kites" of *S. enflata, S. hexaptera, S. serratodentata* and *P. draco,* perhaps indicating a residual reaction to midday light or a period of inequilibrium. Small numbers of *S. serratodentata* and *S. enflata* remained at the surface even during midday.

Spawning—Evidence which suggests that several species breed more or less throughout the year, although usually with definite seasonal maxima, was found. These are *S. enflata, S. serratodentata, P. draco, K. pacifica* and the two neritic species, *S. hispida* and *S. helenae* for which Pierce (1951) gives more extensive data than that obtained at the NG station. Only *S. bipunctata* and *S. minima* appeared not to breed year around. Owing to lack of data, no conclusions were reached as to the breeding periods of the remaining species.

There is reason to believe that those species which occur both in tropical oceanic waters and in colder waters may mature at a smaller size in the former areas. Thomson (1947) has given the only information on mature (stage IV) size of species common to colder (Australian) waters and the Florida Current. It is unfortunate, however, that Thomson used such large size-intervals. For example, he recorded mature *S. enflata* as measuring between 5-10 mm and 20-25 mm; at the NG station, the observed range was 11-29.7 mm. The smallest mature size of most species was markedly less in Florida Current specimens: *S. bipunctata,* Florida Current, 8.5 mm, Aus-

tralia, 10-12 mm; *S. hexaptera,* 27 mm (stage IV) vs 45-50 mm (stage III); *S. serratodentata,* 6 vs 10-12 mm; *S. minima,* 4.7 vs 7-8 mm; *S. decipiens,* 8.8 vs 10-12 mm; *P. draco,* 5.2 vs 8-10 mm; and *K. pacifica,* 4.2 vs 7-8 mm.

The data also indicate that several species spawn more than once in a lifespan. There is no reason to believe that this is restricted to these species in tropical and subtropical areas, although it may be that because of earlier maturation they spawn more often there than in colder waters.

Thus in the Florida Current off Miami, chaetognaths in general may mature at a smaller size than in colder waters, breed to some extent all year long, and spawn more than once in a lifetime. Even so, abundance is very low compared with that of colder waters where marked seasonal changes in availability of nutrients occur, and annual productivity in the southern part of the Florida Current probably no more than equals that of the latter areas.

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PARASITIC COPEPODA FROM MEXICAN COASTAL FISHES

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ABSTRACT

Twenty-five genera and 46 species of parasitic copepods are reported from marine fishes of Mexico. Two new species: *Telson nicholsi* (Taeniacanthidae) and *Thysanote goodi* (Lernaeopodidae) are described.

This report is based upon four collecting trips to the Mexican coasts during the summers of 1954 through 1957. On the Gulf of Mexico, Tampico, Tuxpan, Veracruz, and nearby fishing villages were visited, and on the Pacific Coast, Ensenada and San Felipe in Baja California, and Guaymas, Mazatlan, San Blas, Acapulco, Salina Cruz, and Tehuantepec were visited. Most of these mainland Pacific Coast ports and Veracruz were visited two or more times during this survey. The fish examined were mainly those caught either by sportsmen or by market fishermen, supplemented by visits to fish markets and fish storage houses.

The results have been disappointing. We were able to examine only a relatively few fishes. Sportfishermen are interested in a very limited number of kinds of fishes, and only rarely bring in other than gamefishes. The market fishermen are obviously interested in just a few species of fishes for which there is a sale. Efforts to hire them to catch other kinds were not very successful. Sometimes we were not welcome in the markets, and when we were, the custom of removing the gills meant that so many parasites were lost. We never succeeded in examining the trash fish caught by shrimpers. Although the list of Mexican coastal fishes is both long and interesting, we feel that other methods must be used. Hook and line fishing, skin diving, and if one could afford the risk of loss of gear, the use of nets seem possibilities. More interest in the parasites of fish by Mexican ichthyologists might be very productive.

I wish, first of all, to thank my wife, Dr. Nell Bevel Causey, for her continued and essential assistance, both in the collection of the parasites and in the identification of the hosts. She found most of the parasites and took care of most of the interminable discussions in Spanish necessary for the work. I also thank Dr. G. D. Nichols, Dean of the College of Arts and Sciences, University of Arkansas, for his long continued interest and support of the work, and Dr. V. W.

Adkinson, Dean of the Graduate School, University of Arkansas, for a supplementary grant for the 1957 collecting trip. The many Mexicans, both officials and ordinary citizens, who helped in all ways possible have my deep thanks but must remain unnamed. Dr. C. Bolivar and Dr. Jorge Carranza of Mexico City, and Dr. Miguel Alvarez del Toro of Tuxtla Gutierrez, must, however, be thanked for their interest and aid. I am, of course, pleased to acknowledge the good natured courtesies of my fellow countrymen we met in Mexico.

Although I have little doubt that the majority of the parasitic copepods which have been reported from the United States portion of the Gulf of Mexico, and likewise the majority of parasitic copepods reported from the California coast will ultimately be found in Mexican waters, the following list is restricted to the parasites either reported by other investigators or by the present author as having been taken in Mexican waters. Most of these will be included in the author's projected monograph on the parasitic Copepoda of the Gulf of Mexico. The classification adopted is taken from Wilson's Copepods of the Woods Hole Region (1932). I feel that I must add that I am admittedly a "lumper," and not a "splitter." Many of the groups are in a rather chaotic condition, taxonomically speaking, *e.g.,* the Argulidae, and it seems unwise to add to the confusion by describing all slight variations as new species. Excellent as Dr. Wilson's work was, many of his genera and species are being rejected by later workers. The common names of the fishes are those listed by the American Fisheries Society, except for extralimital forms not covered in its checklist. Spanish names in parentheses are those used by the fishermen; often the same name is applied to several kinds of fishes.

SUBORDER ARGULOIDA

Family Argulidae

Genus *Argulus* Müller, 1785

Argulus chromidis Krøyer, 1863

Reported by Wilson (1936) from *Rhamdia sp.,* Xanaba Cenote Chico, Yucatan. It was "a single female taken from the intestine . . . and was probably a parasite upon some fish eaten by the Rhamdia . . ."

Argulus megalops Smith, 1873

Two collections: a young female from the stargazer, *Astroscopus zephyreus,* at Cholla Bay, near Puerto Penasco, Sonora; and an

immature specimen discovered in a vial with a leech taken from the snook (robalo pardo) *Centropomus undecimalis,* in a fish market at Alvarado, Veracruz. This could have come from any one of several kinds of fish in the market.

Argulus rhamdiae Wilson, 1936

Reported by Wilson (1936) from the skin of *Rhamdia sp.,* Scan Yui Cenote, Yucatan.

SUBORDER CYCLOPOIDA

Family Clausidiidae

Genus *Pherma* Wilson, 1923

Pherma curticaudatum Wilson, 1923

Reported by Wilson (1923): "Three adult females, one with egg strings, taken from the parapodia of an unnamed annelid dredged from a depth of 645 fathoms by the Bureau of Fisheries steamer ALBATROSS off the coast of Lower California in April, 1911."

Family Ergasilidae

Genus *Ergasilus* Nordman, 1832

Ergasilus lizae Krøyer, 1863

From striped mullet (lisa), *Mugil cephalus,* Mazatlan, Sinaloa; San Blas, Nayarit; and Bocco del Rio near Veracruz.

Ergasilus mugilus Vogt, 1877

From *Mugil cephalus,* Tampico, Veracruz; Bocco del Rio near Veracruz; San Blas, Nayarit.

Both of these species are common on the mullet gills, which often look as though they had been peppered.

Family Bomolochidae

Genus *Bomolochus* Nordmann, 1832

Bomolochus attenuatus Wilson, 1913

From white croaker (corvina), *Genyonemus lineatus,* and spotfin croaker, *Roncador stearnsi,* at Ensenada, B. C.; and from California scorpion fish, *Scorpaena guttata,* at Cholla Bay near Puerto Penasco, Sonora.

Bomolochus cincinnus Wilson, 1911

From machete, *Tylosurus sp.,* at Acapulco, Guerrero.

Bomolochus nitidus Wilson, 1911

From *Mugil cephalus,* at Mazatlan, Sinaloa.

Bomolochus soleae Claus, 1864

From Pacific barracuda, *Sphyraena argentea;* California corbina (corvina), *Menticirrhus undulatus;* kelp bass, *Paralabrax clathratus,* and sand bass (cabrillo), *P. nebulifer;* California halibut, *Paralichthys californicus,* and several recorded as "flounders," at Ensenada, B. C.; "flounder," at Cholla Bay near Puerto Penasco, Sonora; and halibut, *Paralichthys sp.,* at Salina Cruz, Oaxaca.

On the United States portion of the Gulf of Mexico I have found *Ergasilus* more common than *Bomolochus.* My Mexican collections are too few to be significant, but *Bomolochus* appears to be the more common genus of the family on the Pacific Coast.

Family Taeniacanthidae

Genus *Telson* Pearse, 1952

Telson nicholsi, n. sp.

Figure 1

This species is, in general, like the type of the genus, *Telson elongatus* Pearse, 1952. The differences are summarized as follows:

T. elongatus	*T. nicholsi, n. sp.*
1st antennae with 4 segments	1st antennae with 6 segments
Maxilliped with a large hook and two hooklets	Maxilliped with a large hook, but no hooklets
4th leg with 2 terminal setae on each branch	4th leg with 4 terminal setae
5th leg with 3 segments and 2 terminal setae	5th leg not segmented and with 2 terminal setae
Abdomen of 1 segment	Abdomen of 3-4 segments, usually 4
Host: *Astroscopus y-graecum*	Host: *Astroscopus zephyreus*
Type locality: Texas coast, Gulf of Mexico	Type locality: Cholla Bay, near Puerto Penasco, Sonora.

Dr. Pearse gave the following dimensions for *T. elongatus:* Length of entire body, 3.8 mm; length of cephalothorax and free thorax, 1.5 mm, width of cephalothorax, 0.58 mm; length, 0.39 mm; length

of abdomen, 2.3 mm. I presume these are averages for his four specimens. The corresponding sizes for *T. nicholsi* are: Length of entire body, 5.86 (4.8-6.8) mm; length of cephalothorax and free thorax,

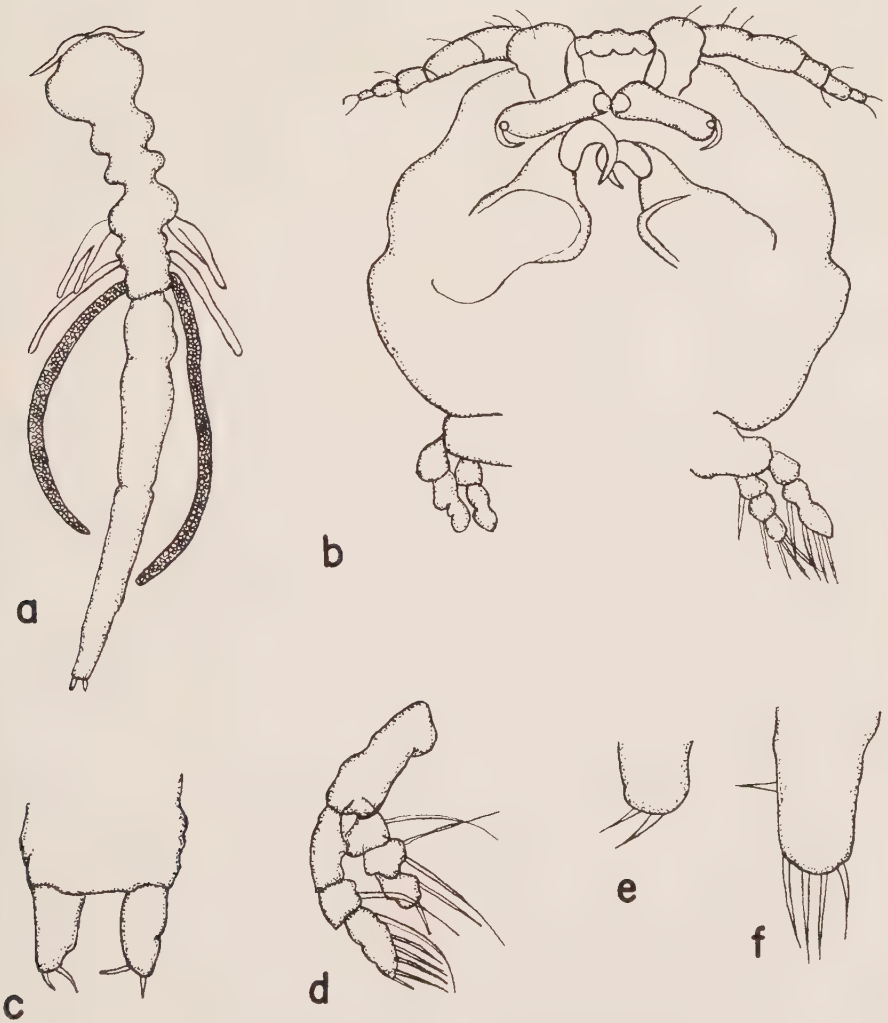

FIGURE 1. *Telson nicholsi*, n. sp. a, Dorsal view of the body. No attempt was made to indicate the portions of the first three pairs of legs which are visible from this view. b, Ventral view of the cephalothorax showing the 1st and 2nd antennae, the maxillipeds, and posteriorly, the 1st pair of legs. c, The caudal rami. d, The 3rd leg. e, End of the 5th leg. f, End of one branch of the 4th leg.

1.9 (1.3-2.6) mm; width of cephalothorax, 0.7 (0.5-0.8) mm; length, 0.58 (0.4-0.7) mm; length of abdomen, 3.13 (2.5-3.6) mm. These are averages for the first 10 straight specimens encountered, with minimal and maximal sizes in parentheses. 144 females were collected from the ventral surface near the pelvic fins of the host. The copepods had orange colored bodies and white egg strings. No males were found. The types are deposited in the U. S. National Museum, catalog numbers 101207 and 101208.

The species is named for Dr. G. D. Nichols, Dean of the College of Arts and Sciences, University of Arkansas, whose encouragement and financial assistance have made so much of my recent work possible.

SUBORDER CALIGOIDA

Family Caligidae

Genus *Anuretes* Heller, 1865

Anuretes heckelii Krφyer, 1863

From Atlantic spadefish (chavel), *Chaetodipterus faber,* on the gills and in the opercular chamber, at Tuxpan, Veracruz. This species is common on the spadefish, but occurs on other fishes.

Genus *Caligus* Müller, 1785

Caligus bennetti Causey, 1953

From the mouth of bacaco, a spotted sand bass, *Paralabrax maculatofasciatus,* at Mazatlán, Sinaloa; and from Bermuda chub (chopa blanca), *Kyphosus sectatrix,* operculum at a Veracruz fishmarket.

Caligus bonito Wilson, 1905

From the mouth of the Pacific bonito, *Sarda chiliensis,* at Salina Cruz, Oaxaca. A chalimus stage from *Lutjanus sp.,* Mazatlan, Sinaloa, is probably of this species.

Wilson (1905) reported this species from a grouper, *Cratinus agassizii,* and a red snapper, *Lutjanus novemfasciatus,* Tangola, Mexico.

Caligus constrictus Heller, 1865

From the Crevalle jack (toro), *Caranx hippos,* Mazatlan, Sinaloa; and Acapulco, Guerrero.

Caligus haemulonis (Krφyer), 1863

From the bandera, probably *Bagre marinus,* but my record is incomplete. Collected in the Veracruz fishmarket.

Caligus latifrons Wilson, 1905

From the bullseye puffer, *Sphaeroides annulatus,* at Guaymas, Sonora. This was identified by a Loma Linda scientist.

Caligus mutabilis Wilson, 1905

From Atlantic croaker (corvina), *Menticirrhus undulatus,* at Ensenada, B. C.; sierra, *Scomberomorus sierra,* Pacific porgy (mojarra garabata), *Calamus brachysomus,* the sand bass, *Paralabrax nebulifer,* the kelp bass, *Paralabrax clathratus,* and spotted sand bass, *Paralabrax maculatofasciatus,* at Cholla Bay, near Puerto Penasco, Sonora; sierra, *S. sierra,* and skipjack, tuna, *Euthynnus pelamis,* at Guaymas, Sonora; sierra, *S. sierra,* paperfish, *Selene oerstedii,* and *Mugil cephalus,* at Mazatlan, Sinaloa; robalo, *Centropomus sp.,* at San Blas, Nayarit; Pacific bonito, *Sarda chiliensis,* and triggerfish, *Balistes sp.,* Acapulco, Guerrero; and Pacific spadefish, *Chaetodipterus zonatus,* at Salina Cruz, Oaxaca.

Caligus pelamydis Krøyer, 1863

From king mackerel, *Scomberomorus cavalla,* Veracruz, Veracruz.

Caligus productus Dana, 1854

From the yellowtail, *Seriola dorsalis,* and kelp bass, *Paralabrax clathratus,* at Ensenada, B. C.; spotted sand bass, *Paralabrax maculatofasciatus,* a triggerfish, *Verrunculus polylepis,* a mackerel, and two females in a collection of small decapods, a snail and a brittlestar from the beach at Cholla Bay, near Puerto Penasco, Sonora; the skipjack, *Katsuwonus vagans,* the barracuda, *Sphyraena argentea,* sierra, *Scomberomorus sierra,* and dolphin, *Coryphaena sp.,* at Guaymas, Sonora; bacaco, an unidentified seabass, and the majarra, *Calamus brachysomus,* at Mazatlan, Sinaloa; red snapper, *Lutianus sp.,* at San Blas, Nayarit; dolphin, *Coryphaena hippurus,* at Acapulco, Guerrero; and snook, *Centropomus sp.,* at Salina Cruz, Oaxaca.

It would appear from these records that *Caligus mutabilis* and *C. productus* are the two common species on the Pacific coast, and that there is little host specificity. Most unexpected was the discovery of the two *C. productus* in a beach collection. Caligids are often found in the plankton, and their presence on the beach is easily understood.

Genus *Caligodes* Heller, 1865

Caligodes laciniatus (Krøyer), 1863

Two collections one from the barracuda, *Sphyraena argentea,* at

Guaymas, Sonora; and one from the machete or needlefish, not identified, at Acapulco, Guerrero.

Genus *Lepeophtheirus* Nordman, 1832

Lepeophtheirus dissimulatus Wilson, 1905

From the California hake, *Merluccius productus,* the California halibut, *Paralichthys californicus,* the diamond turbot, *Hypsopsetta guttulata,* and barracuda, *Sphyraena argentea,* at Ensenada, B. C.; the rock bass, *Paralabrax nebulifer,* at Cholla Bay near Puerto Penasco, Sonora; the puffer (cf. statement under *Caligus latifrons supra),* and catfish, *Galeichthys guatemalensis?,* at Mazatlan, Sinaloa.

Lepeophtheirus thompsoni Baird, 1850

From the white seabass (corvina), *Cynoscion nobilis,* at Cholla Bay near Puerto Penasco, Sonora; Guaymas, Sonora; San Blas, Nayarit; and Acapulco, Guerrero.

This genus is common along the United States portion of the Gulf of Mexico, and its absence along the Mexican portion can only mean inadequate collecting. An opportunity to examine fish *with gills* would change this!

Family Euryphoridae

Genus *Gloiopotes* Steenstrup and Lütken, 1861

Gloiopotes costatus Wilson, 1919

From the Pacific sailfish, *Istiophorus greyi,* at Guaymas, Sonora; and at Mazatlán, Sinaloa; and from the marlin, *Makaira sp.,* at Acapulco, Guerrero. One of the specimens collected at Mazatlán had the barnacle *Conchoderma* upon it. One Acapulco collection was sent to me by Mr. Terrance R. Leary, Rockport, Texas. This species of copepod was originally described by Wilson from a "swordfish" at Catalina Island, off the coast of California. Presumably, his use of quotation marks indicates some doubt as to the host. It is quite common on the sailfish and marlin along the Mexican Pacific coast. The blue bodies and red egg strings are quite conspicuous.

Family Pandaridae

Genus *Achtheinus* Wilson, 1908

Achtheinus oblongatus Wilson, 1908

From the bay shark, *Carcharhinus lamiella,* at Cholla Bay, near

Puerto Penasco, Sonora. This parasite was originally described by Wilson from the leopard shark, *Triakis semifasciata,* with La Jolla, California the type locality. This present record appears to be the second.

Genus *Perissopus* Steenstrup and Lütken, 1861

Perissopus communis Rathbun, 1887

From an unidentified shark, 6 feet long, examined at Acapulco, Guerrero. A single male was examined.

Genus *Pandarus* Leach, 1816

Pandarus bicolor Leach, 1816

From an unidentified shark at Acapulco, Guerrero. It was called a "flying shark," a common name I do not find in the literature.

Genus *Nesippus* Heller, 1865

Nesippus alatus Wilson, 1907

From the bay shark, *Carcharhinus lamiella,* at Cholla Bay, near Puerto Penasco, Sonora.

Family Anthosomidae

Genus *Lernanthropus* Blainville, 1822

Lernanthropus gisleri van Beneden, 1852

From the snook (chucumita), *Centropomus undecimalis,* at Tuxpan, Veracruz.

Lernanthropus micropterygis Richiardi, 1882

Reported by Wilson (1937) from the gills of the greater amberjack, *Seriola dumerili,* at White Friars, Mexico.

Lernanthropus pomatomi Rathbun, 1887

From pargo, *Lutjanus sp.,* at Mazatlán, Sinaloa; and from huracha (which may be a local version of jurel), the horse mackerel, *Trachurus trachurus,* at San Blas, Nayarit.

Family Eudactylinidae

Genus *Krφyeria* van Beneden, 1853

Krφyeria papillipes Wilson, 1937

Reported by Wilson (1937) from a gray shark, Socorro Island, Mexico.

Family Pseudocycnidae

Genus *Pseudocycnus* Heller, 1865

Pseudocycnus appendiculatus Heller, 1865

Four collections from the Pacific bonito, *Sarda chiliensis,* at Acapulco, Guerrero.

Pseudocycnus buccatus Wilson, 1922

From cero (peto), *Scomberomorus regalis,* Spanish mackerel (sierra), *S. maculatus,* and king mackerel, *S. cavalla* at Veracruz; from *S. regalis* at Anton Lizardo near Veracruz; and from the Mexican sierra, *S. sierra,* and kelp bass, *Paralabrax maculatofasciatus,* at Cholla Bay near Puerto Penasco, Sonora.

Members of this genus are very common on the gillets or demibranchs, where patches as large as one's thumb nail are often present. The Pacific forms may be slightly smaller than the Gulf of Mexico representatives.

Family Dichelesthiidae

Genus *Hatschekia* Poche, 1902

Hatschekia albirubra Wilson, 1913

From the kelp bass, *Paralabrax clathratus,* and California corbina (corvina), *Menticirrhus* undulatus, at Ensenada, B.C.

Hatschekia oblonga Wilson, 1913

From the yellowtail snapper (rubia), *Ocyurus chrysurus,* at Anton Lizardo near Veracruz.

Family Lernaeidae

Genus *Lernaeenicus* LeSueur, 1824

Lernaeenicus longiventris Wilson, 1917

From yellowtail, *Seriola dorsalis,* at Mazatlán, Sinaloa. This copepod, because of its length, attracts attention and is well known to fishermen. It is common along the United States Gulf of Mexico.

Family Pennellidae

Genus *Pennella* Oken, 1816

Pennella filosa (Linnaeus), 1758

From the Pacific sailfish, *Istiophorus greyi,* at Guaymas, Sonora;

Mazatlán, Sinaloa; and Acapulco, Guerrero. This large copepod is often encrusted with the barnacle *Conchoderma* and is quite conspicuous. We got the largest numbers at Guaymas, probably because more sailfish happened to be caught during our visit.

SUBORDER LERNAEOPODOIDA

Family Chondracanthidae

Genus *Acanthochondria* Oakley, 1927

Acanthochondria albigutta Pearse, 1952

From mangalla, *Paralichthys sp.*, at Salina Cruz, Oaxaca.

Family Lernaeopodidae

Genus *Thysanote* Krøyer, 1863

Thysanote goodi, n. sp.

Figure 2

This species, which I describe as new with some hesitancy, is based upon a single specimen obtained from the mouth of the great barracuda, *Sphyraena barracuda,* at Anton Lizardo, near Veracruz. In view of my having but one specimen, no attempt has been made to work out the mouth parts. It is deposited in the U.S. National Museum, No. 101209.

The specimen has a body length of 5 mm, with the egg strings 3 mm in length. If the specimen had lacked the egg strings I would have regarded it as an immature, possibly aberrant, *T. appendiculata* (Steenstrup and Lütken), 1861, to which it keys out in Wilson's (1915) key. The pertinent difference is in the processes which hang from the posterior margin of the second maxilla. *T. appendiculata* has four processes hanging from the border of each maxilla, while *T. goodi, n. sp.,* has but a single process on each maxilla. In *T. appendiculata* the length of these processes appears to vary; fig. 35 of Steenstrup and Lütken has a ventral view in which the medial pair of processes on the left side are about half the length of the lateral pair. Both species appear to agree in lacking processes attached to the body at the base of the maxillae, which Wilson lists as a generic character; and agree in the number of processes at the posterior end of the body. These processes appear to be relatively longer in *T. appendiculata* than in *T. goodi, n. sp.* The species is named for my

longtime friend and associate, Mr. William J. Good of the University of Arkansas.

With this species as a starting point a rather interesting series can be arranged for the genus: *T. goodi, n. sp.* and *T. appendiculata* differing in the number of unbranched processes; and then *T. longimana, T.*

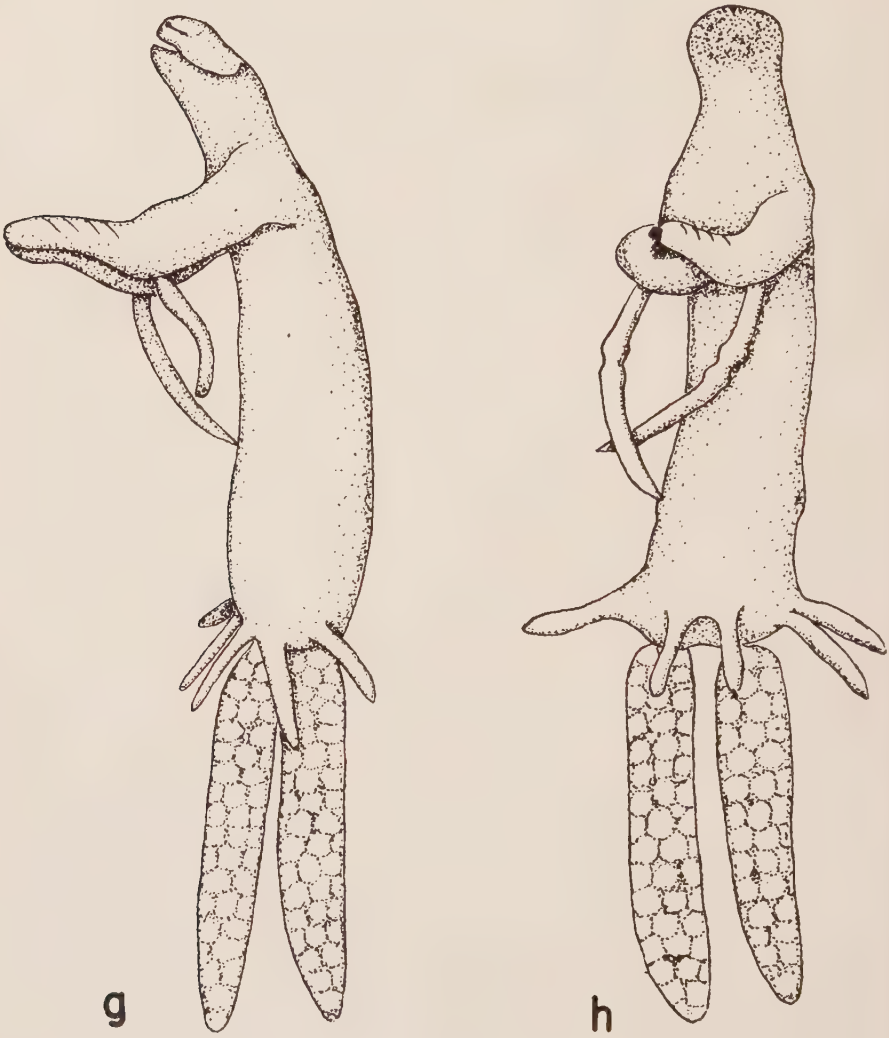

FIGURE 2. *Thysanote goodi,* n. sp. a, Lateral view. b, Ventral view.

lobiventri (with which *T. trilobate* may be identical), and *T. pomacanthi* in which the processes become progressively more and more branched.

Thysanote longimana Wilson, 1913

From pargo colorado, *Lutianus colorado,* Mazatlán, Sinaloa; San Blas, Nayarit; and Salina Cruz, Oaxaca; and from yellowtail snapper (rubia), *Ocyrus chrysurus,* at Anton Lizardo near Veracruz.

Genus *Naobranchia* Hesse, 1863

Naobranchia lizae (Krφyer), 1863

From *Mugil cephalus,* at Mazatlán, Sinaloa.

Anchorella Krφyer, 1837

Anchorella urolophi Krφyer, 1863

Reported by Krφyer (1863) off the Mexican coast. Wilson (1915) seemed to doubt the validity of this genus, and to regard it as synonymous with *Clavella.* He furthermore did not think that this species can be placed in the genus *Clavella.* Until additional specimens are found for study, it must remain uncertain as to validity and taxonomic position.

Genus *Brachiella* Cuvier, 1830

Brachiella gracilis Wilson, 1908

From ocean whitefish, *Caulolatilus princeps,* at Ensenada, B.C.; from berrugate, probably a local name for *C. princeps,* at Mazatlán, Sinaloa; from alacron, *Menticirrhus nasus?,* Salina Cruz, Oaxaca; and from the white croaker, *Genyonemus lineatus,* at Tehauntepec, Oaxaca, fishmarket.

Brachiella gulosa Wilson, 1915

From spotfin croaker, *Roncador stearnsi,* at Ensenada, B.C.

Brachiella sciaenophila Heller, 1865

A single specimen from a croaker, *Roncador stearnsi?,* at Ensenada, B.C.

Summary

Some 25 genera and 46 species of parasitic copepods are reported from fish of Mexican coastal waters, two of the species being new. This is disappointing and unsatisfactory, and shows how inadequate

the survey has been. To indicate the status of the "inventory" the following table is offered as approximately correct. The so-called semiparasitic copepods are omitted, and very few from invertebrates are included.

TABLE 1

PARASITIC COPEPODA FROM NORTH AMERICAN WATERS

Author	Locality	No. Genera	No. Species
Bere (1936)	Lemon Bay, Fla.	34	68
Causey (1953a)	Grand Isle, La.	15	24
Causey (1953b)	Port Aransas, Texas	23	45
Causey (1955)	Pascagoula, Miss.	22	30
Krøyer (1863)	New Orleans, La.	8	9
Pearse (1947, 1948)	Beaufort, N. C.	28	36
Pearse (1951)	Bimini, Bahamas	10	24
Pearse (1952a)	Port Aransas, Texas	33	56
Pearse (1952b)	Alligator Harbor, Fla.	25	47
Wilson (1913)	Jamaica	24	52
Wilson (1932)	Woods Hole, Mass.	69	121
Wilson (1935)	Dry Tortugas	28	37
Causey	Mexican Coasts	25	46

My checklist of the Gulf of Mexico copepods shows that 78 genera and 232 species (not including a few so-called semiparasitic species) have been reported, practically all having been found by two or more investigators. Most of these might well be expected to occur also on fish along the Mexican Gulf of Mexico. This is worth noting, as most of my Mexican records are from the Pacific Coast.

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SALINITY AS A FACTOR IN THE CONTROL OF GROWTH AND SURVIVAL OF POSTLARVAE OF THE SOUTHERN FLOUNDER, *PARALICHTHYS LETHOSTIGMA*

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Abstract

Study of the effect of a range of salinities on growth and survival of postlarvae of *Paralichthys lethostigma* Jordan and Gilbert under laboratory conditions indicates good survival without acclimatization in salinities ranging from 0‰ to 30‰. Growth appears to be influenced by salinity with greater weight increase per unit of time occurring under more saline conditions.

Introduction

Brown (1957) states that food supply is probably the most potent factor affecting growth of fishes. She states further that although environmental factors such as temperature, light, and space have been shown to affect growth, no one has demonstrated unequivocally that fish growth rates are affected directly by the ionic composition of the water. Salmonids which migrate show a great increase in growth in ocean waters, but Brown (1957) points out that this may be due to differences in food supply rather than to differences in water composition. Canagaratnam (1959) reviews the literature concerned with relationships between growth and salinity and finds that in ten out of eleven species, marine- and brackish-water inhabitants are larger than inhabitants of fresher waters. He points out further that several experiments including work on the whitefish, *Coregonus clupeaformis,* (Rawson, 1946), the sockeye salmon, *Oncorhynchus nerka,* (Foerster, 1947), preadult growth of the guppy, *Lebistes reticulatus,* (Gibson and Hirst, 1955) indicate that better growth occurs in more saline waters. From his experiments in which temperature and food were controlled, Canagaratnam (1959) concludes that coho salmon fry, *Oncorhynchus kisutch,* grow faster in higher salinities. He attached no significance to results obtained with sockeye salmon and chum salmon, *Oncorhynchus keta* because of too few data. He reports no appreciable difference in growth of mature goldfish in fresh water and 6‰ salinity.

The present study is concerned with salinity as a factor in the control of survival and growth of postlarvae of the southern flounder, *Paralichthys lethostigma.* Although the species has often been con-

fused with *P. dentatus* and *P. albigutta,* its validity has been clearly established by Ginsburg (1952). It is now known to occur in marine and estuarine waters from the Albemarle Sound region of North Carolina to Corpus Christi Pass, Texas.

P. lethostigma is a highly euryhaline species. Smith (1907) reports that individuals are not uncommon in the western end of Albemarle Sound, N. C., and they have been found to ascend considerable distances into fresh water in the Roanoke River above Plymouth, N. C. Gunter (1945) reports capture of the species in Texas in salinities ranging from 2.0‰ to 36.2‰. The author has collected specimens in North Carolina waters whose salinities ranged from 0.9‰ to 30.0‰ in all types of environments from small, tidewater creeks to broad rivers and sounds over bottoms ranging from mud to predominantly sand.

Because of the apparent wide salinity tolerance of *P. lethostigma* in nature and the relative ease with which postlarvae can be collected and reared in the laboratory (Deubler, 1958), an experiment was designed to determine the effect of a range of salinities on survival and growth of postlarvae under laboratory conditions.

The writer thanks Dr. Bernard Pasternack, Department of Biostatistics, University of North Carolina for counsel concerning the statistical treatments, Dr. Gerald S. Posner who performed weight measurements, Brian J. Rothschild for counsel and performing some of the computations, and colleagues who offered valuable suggestions concerning the manuscript.

Materials and Methods

The term postlarvae as used in this paper includes individuals that have completely absorbed the yolk sac but have not developed the definitive characters of the species (Hubbs, 1943).

During the night hours of winter months, postlarvae of *Paralichthys* (*dentatus, albigutta* and *lethostigma*) can be collected in a viable state from the surface waters of Bogue Sound in the vicinity of Beaufort and Morehead City, N. C. Postlarvae for this study were collected by anchoring a 46-foot research vessel in a strong flood tide, after dark, and setting a conically-shaped, nylon net (mouth diameter, 152 cm; mesh size, 1.5 mm) from the stern. The tidal current was sufficiently strong to hold the net at the surface of the water. A two-quart glass collecting jar was secured to the terminal open end of the net in order to trap postlarvae in water. After intervals

of approximately fifteen minutes in the water, the net was withdrawn and the contents of the jar and terminal end of the net were washed into an open bucket in order to dilute the sample. The contents of the bucket were gradually emptied into a shallow, white, enamel-coated sorting tray and the flounder postlarvae were transferred by means of an aspirator to a 5-gallon glass bucket containing sea water from the site of capture (salinity, 30‰, temperature, 10°C). During the entire operation the postlarvae were constantly in water.

The postlarvae were taken to the laboratory where they were anesthetized lightly with tricaine methanesulfonate (M.S. 222) and the postlarvae of *P. lethostigma* were separated from those of *P. dentatus* and *P. albigutta* under a binocular microscope by utilizing differences in pigmentation and fin-ray counts (Deubler, 1958). The postlarvae of *P. lethostigma* were revived by placing them in several changes of untreated sea water. Mortality due to anesthetization was negligible. The entire sample of *P. lethostigma* was then placed in a shallow, enamel-coated sorting tray (39 cm x 23 cm x 6.5 cm) and freshly hatched nauplii of brine shrimp (*Artemia*) were introduced. Those postlarvae which did not feed actively were discarded and, from the remainder, seven subsamples of twenty individuals each were drawn by passing a plastic screen of small mesh size through the sample. It was assumed that each subsample accurately represented the original sample as to size of individuals. No initial weights or lengths were taken of the individuals within each subsample because of the danger of injuring the small postlarvae (length 8-12 mm, S.L.; mean weight, 15 mg after preservation). It was felt that the subsequent experimental error due to injured animals would be far greater than that caused by any slight differences that might exist in initial weights of postlarvae between subsamples.

A subsample was assigned at random to each of seven round glass aquaria containing two gallons of water whose salinities varied by 5‰ and ranged from 0‰ to 30‰. Water of the desired salinity was prepared by diluting natural sea water from the site of capture with tap water. No attempt was made to acclimate postlarvae prior to submersion in lowered salinities.

Two experimental series were established. The first of these was begun 27 January 1959 and terminated 10 March 1959 (42 laboratory days). The second experiment was initiated 10 February 1959 and ended 10 March 1959 (28 laboratory days).

Both series were housed in a constant-temperature room in which

the water temperature in all tanks was 15°C. Light was constant within each series and, following the work of Qasim (1955) which showed that the fry of *Blennius pholis* grow better with 16-17 hours of darkness than in continuous light, the lights were turned off at night.

Postlarvae in both series were fed exclusively on nauplii of brine shrimp (*Artemia*). Feeding was not restricted since the quantity of food introduced was in excess of feeding requirements. Food was available constantly in all tanks at the same density insofar as could be determined by visual observation.

Tanks were cleaned at two-day intervals by stirring vigorously with a glass tube to set the water in motion and siphoning with a soft rubber tube through glass wool to remove particulate matter such as fecal material and dead *Artemia*. A sufficient amount of water was left in each tank to cover the animals. Upon completion of the cleaning operation, the filtered water was returned to the appropriate tanks.

To protect against the accumulation of metabolites one gallon of water was removed from each tank at seven-day intervals and replaced with "new" water of the proper salinity. Such a method allowed for control of metabolites without the necessity of constant filtration through activated charcoal while protecting against too sharp a reduction in metabolites which might lead to distress or even death of the animals. Water in all tanks was undisturbed and no aeration was provided except that which occurred during the mechanics of tank cleaning.

Tanks were examined several times daily for dead flounders. These were removed with an aspirator and fixed in 10-per cent formalin for subsequent study. No flounders were substituted for those which died. Upon termination of the experiments, postlarvae in each tank were killed and fixed in ten-per cent formalin, washed in water, and transferred to a 40-per cent solution of isopropyl alcohol for permanent storage.

Terminal weights were determined to the nearest 0, 1 mg on an analytical balance by a colleague who was not familiar with the histories of the samples. Preparatory to weighing each sample was dried with blotting paper to remove excess alcohol and then placed in a tared vial containing 40-per cent isopropyl alcohol. An average weight rounded to the nearest milligram was computed by dividing the weight of the sample by the total number of flounders in the sample.

To determine whether survival of postlarvae of *Paralichthys lethostigma* was dependent upon salinity of the water in which they were reared, a record of mortality was maintained for each tank for both experiments. Upon termination of the experiments, the number of flounders surviving in each tank was computed. For the purpose of analyzing these data it was hypothesized that survival could be considered as occurring at random and the Chi-square test was applied to this hypothesis (Snedecor, 1956).

Data concerning weights in both experiments were treated according to standard linear regression techniques (Snedecor, 1956).

Discussion

Postlarvae of *Paralichthys lethostigma* are voracious feeders under laboratory conditions and consume nauplii of *Artemia* readily with no indication of satiety. With the exception of those reared in fresh water, all postlarvae tended to gorge themselves and it was necessary to feed frequently in order to maintain dense concentrations of *Artemia* in the tanks. Postlarvae reared in fresh water showed a noticeable reduction in appetite and, although they fed actively, it was not necessary to introduce food as often as in the other tanks to maintain a dense concentration.

Survival of postlarvae in all tanks for both the 28-day and 42-day experiments was good (Table 1) and suggests that the initial, abrupt transfer of postlarvae from natural waters of high salinity (30‰) to water varying from 0‰ to 25‰ with no previous acclimatization had no obvious influence upon survival for the time periods involved. Applying the Chi-square test at P .05, 6 d.f., the values observed (Table 1) support the hypothesis that survival could be considered as occurring at random in both the 28-day and the 42-day experiments.

TABLE 1
Survival and Growth of Postlarvae of *Paralichthys lethostigma* Under Conditions of Varying Salinity

	Salinity ‰							
	0	5	10	15	20	25	30	X^2
28 laboratory days								
No. of survivors	20	19	20	18	20	20	20	0.19
Mean wt., nearest mg	34	34	38	41	42	46	44	
42 laboratory days								
No. of survivors	15	20	17	20	19	20	18	1.20
Mean wt., nearest mg	53	54	62	52	61	59	72	

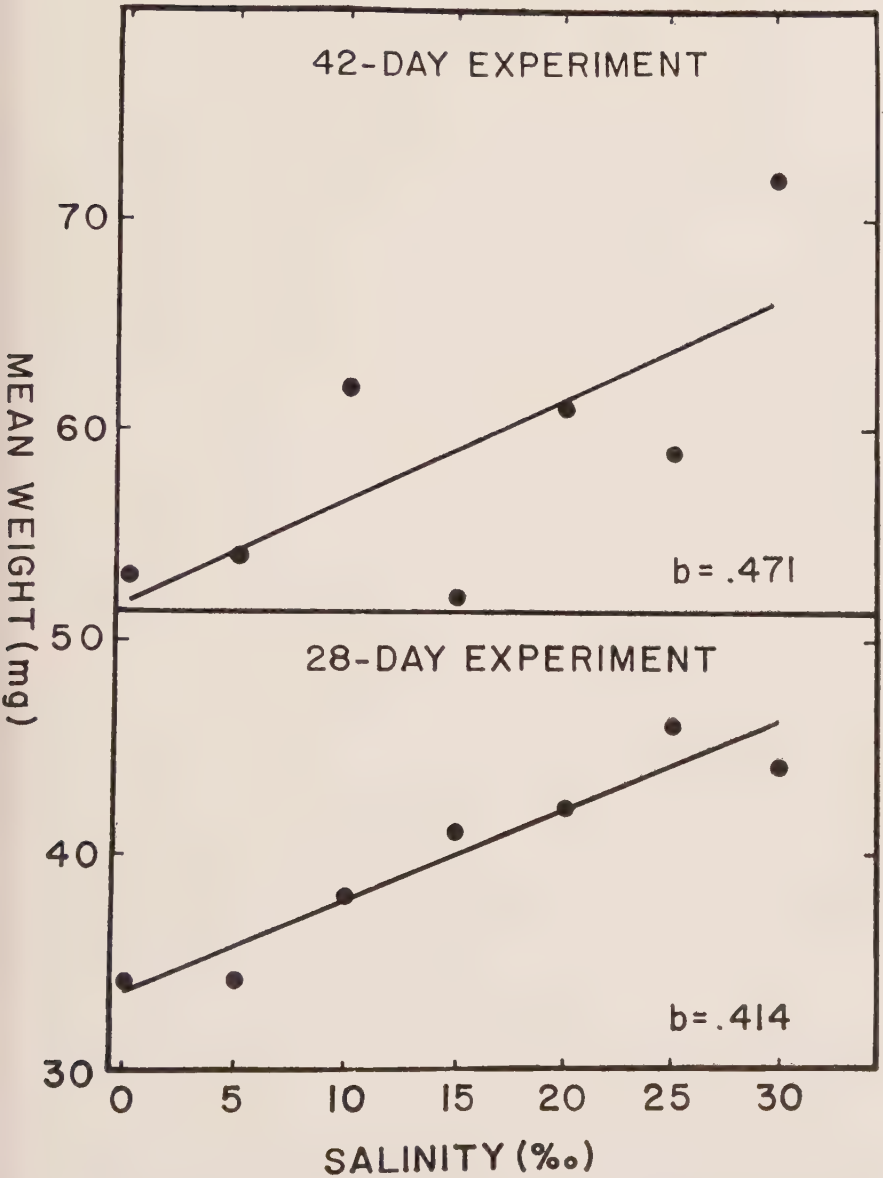

FIGURE 1. Relationship between terminal, mean weight (mg) and salinity in laboratory-reared postlarvae of *Paralichthys lethostigma.*

The application of linear regression techniques in the 28-day experiment to average terminal weights of samples reared in different salinities indicate strongly that salinity exerted a marked influence on growth of postlarvae under laboratory conditions and that postlarvae reared under more saline conditions tended to gain more weight on the average in the same period of time (Fig. 1). An analysis of variance of the regression components, regression (weight on salinity) and deviations from regression, yielded an F value of 47.30 ($F_{.005} = 22.78$). Weight accounted for 90.4% of the variation about the regression line.

In the 42-day experiment, the effect of salinity on weight is not so clearly demonstrated as is noted by the increased variation about the regression line (Fig. 1), and an analysis of variance of the regression components yielded an F value of 5.70 ($F_{.05} = 6.61$). Weight accounted for 53.2% of the variation about the regression line. Although the F value does not quite attain the 5% level of significance, evidence does exist to support a linear relationship between salinity and growth. The increased variation about the regression line in the 42-day experiment is probably accounted for not by any decrease in the effect of salinity on growth, but rather by the fact that the increased time interval of the experiment has allowed uncontrolled factors, *e.g.* crowding and increased variance in size of flounders, to exert an influence that tends to mask the effect of salinity.

Figure 1 shows that regression coefficients (b) for the 28-day and 42-day experiments are very similar. An "approximate t" test of significance of the difference between these coefficients gave a value of 0.277 ($t_{.05} = 2.571$) that strongly suggests that the true difference between the two regression coefficients, if any, can be regarded as negligible. That the regression coefficients are essentially the same suggests that the chief factor controlling growth in both experiments is probably the same.

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ENVIRONMENTAL EFFECT ON LEAVES OF *DIPLANTHERA* DU PETIT-THOUARS[1]

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ABSTRACT

Diplanthera was collected from three tidal zones from various Florida locations. Three growth conditions were found which corresponded to these tidal zones. The first, found in areas exposed at both neap and spring low tides, consisted of dwarf-sized plants. The second, found in areas exposed only at spring low tides, were intermediate in size between the first and third classifications. The third condition, found in areas never exposed, displayed plants of luxuriant size. Leaf length, leaf width, rhizome thickness, and rhizome internode length were found to be affected by the environment. The two vegetative characters of leaf apex and internal cellular anatomy were considered by Sauvageau (1890) and later substantiated by Feldmann (1938) as valid for the separation of the two species of *Diplanthera, D. uninervis* and *D. wrightii*. The author found that these factors were variable in *D. wrightii*, according to the tidal zone in which the plants were found. It is concluded that these two characters are not valid for distinguishing the two species.

INTRODUCTION

The two described species of *Diplanthera (D. uninervis* (Forsk.) Aschers. and *D. wrightii* Aschers.) closely resemble each other. Feldmann (1938) stated that it was very difficult to distinguish between the two species in the sterile condition. Sauvageau (1890), however, found that the leaves differ in two ways. At the apex of mature leaves of *D. uninervis,* three points were found (Fig. 1a). These points represent the extension of the three leaf vascular bundles beyond the regular leaf tissue. In *D. wrightii* the midvein in the center of the leaf did not project out. The leaf apex is thus V-shaped (Fig. 1b). Only in very young leaves of *D. wrightii* is a small round point found terminating the midvein. These later decay and fall off, according to Sauvageau *(op. cit.).* Feldmann *(op. cit.)* found that mature leaves of *D. wrightii* from Mauritius and Guadeloupe lacked the projection in the center of the leaf apex. The other difference was observed by taking a transverse section of a mature leaf immediately above the ensheathing portion. Sauvageau *(op. cit.)* found intercellular spaces between the cells situated above and below the median vascular bundle in mature leaves of *D. uninervis* (Fig. 3). In *D. wrightii* these spaces became well defined lacunae (Fig. 2). Feldmann *(op. cit.)* found this latter structure in

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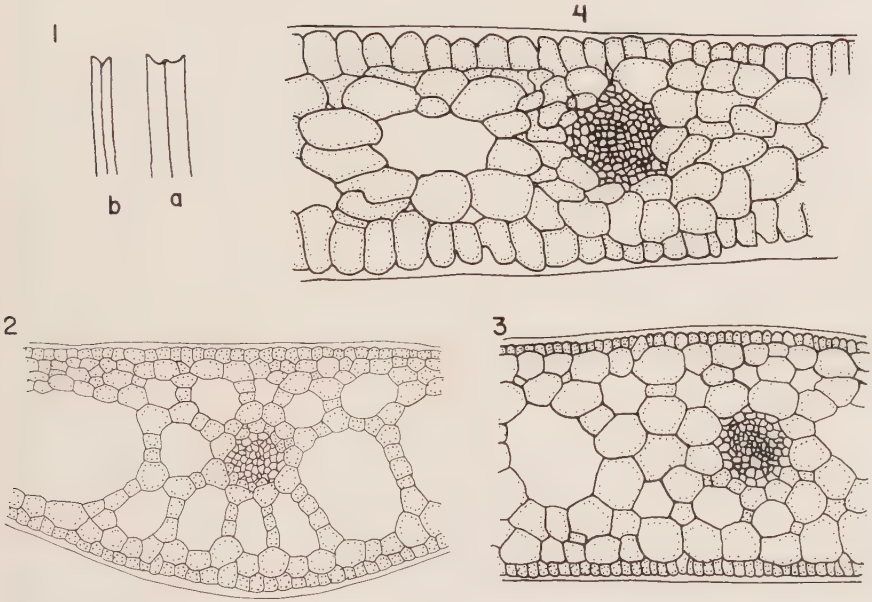


FIGURE 1. Leaf apices of *Diplanthera* (after Sauvageau, 1890). a. Apex of *D. uninervis* leaf, 6X. b. Apex of *D. wrightii* leaf, 6X.

FIGURES 2-3. X-section of *Diplanthera* leaves at base, just above the ensheathing portion. (after Sauvageau, 1890). 500X. Fig. 2. *D. wrightii*. Note large, conspicuous lacunae surrounding midvein. Fig. 3. *D. uninervis*. Note absence of large conspicuous lacunae.

FIGURE 4. X-section of *D. wrightii* leaves at base, just above the ensheathing portions. From zone exposed to air at all low tides, Beach Drive, SE, St. Petersburg, Tampa Bay, October 17, 1958. 640X.

plants collected at Mauritius and Guadeloupe. This zone of intercellular spaces and lacunae around the midvein, according to Sauvageau *(op. cit.),* was narrow. At a level slightly above the ensheathing portion of the leaf the structure of each species became identical. This condition persisted all the way to the leaf apex. The structure at the apex, a genus characteristic, consisted of two internal layers of cells, in contact with and opposite each other, between the upper and lower epidermal cell layers.

DISCUSSION

In the course of research on Florida seagrasses, *Diplanthera* was collected from many locations. It is generally accepted that *Diplanthera wrightii* is the correct name for the species found in Florida and

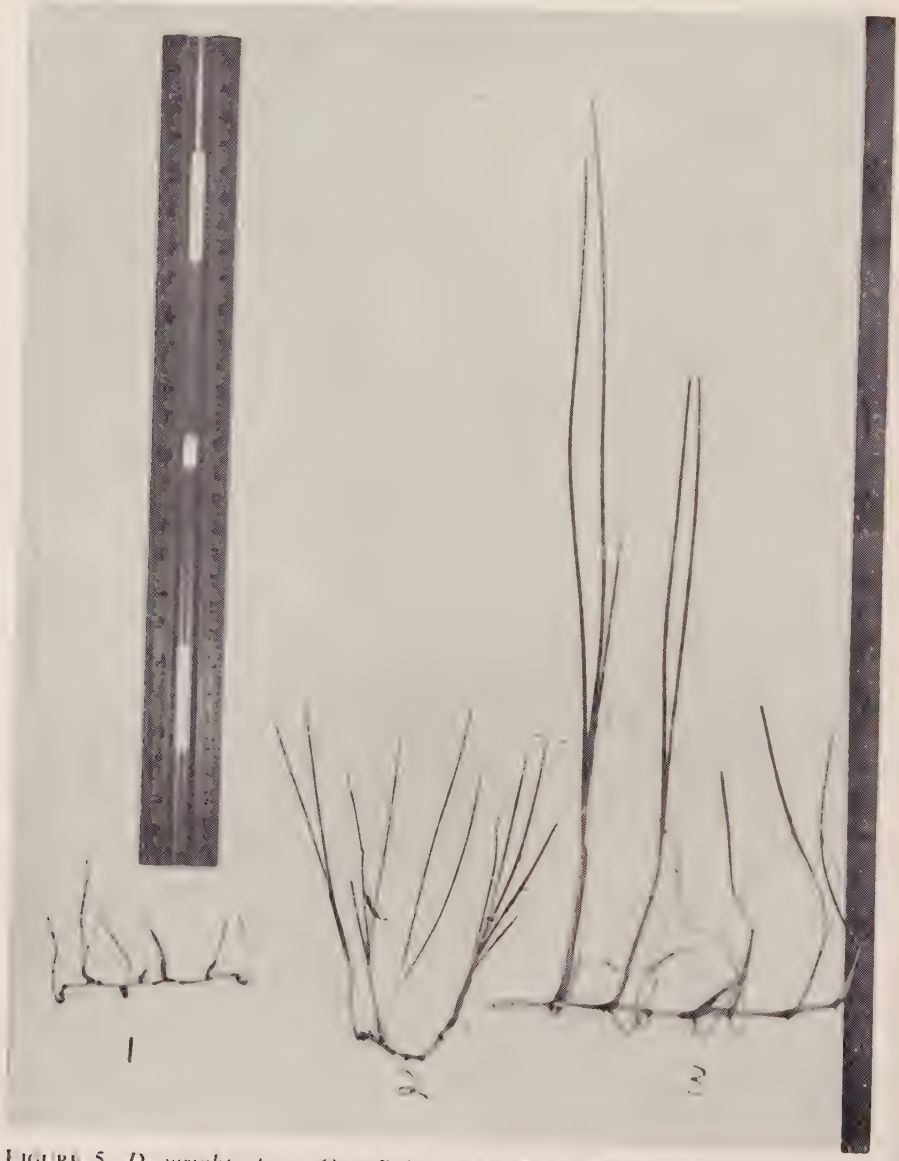


FIGURE 5. *D. wrightii* from Cats Point Bank, Boca Ciega Bay, September 19, 1958. 1. Plants found in zone exposed to air at all low tides. 2. Plants found in zone exposed to air only at spring low tides. 3. Plants found in zone never exposed to air.

throughout the Caribbean area. *Diplanthera uninervis* has been reported from the Red Sea, to the Indian Ocean, and on to the coasts of Australia in the Pacific Ocean.

The author has observed that in very shallow water plants of *Diplanthera* differ in size and habit, according to the tidal zone in which they are found (Fig. 5). All collections were made before winter leaf kill modified conclusions. Observations listed below are specific for a location, but in all instances were confirmed by observations from other areas.

Three growth conditions of *Diplanthera* were found. The first, found in areas which were left exposed to the air at all low tides, consisted of dwarfed plants. The second, intermediate in size between the first and third classifications, were found in areas left exposed only at the spring slack low tides. The third growth condition which displayed long and luxurious leaves was found in areas never uncovered by low tides. Plants found in one foot or ten feet of water at the spring slack low tide appeared to have identical leaf length and plant vigor.

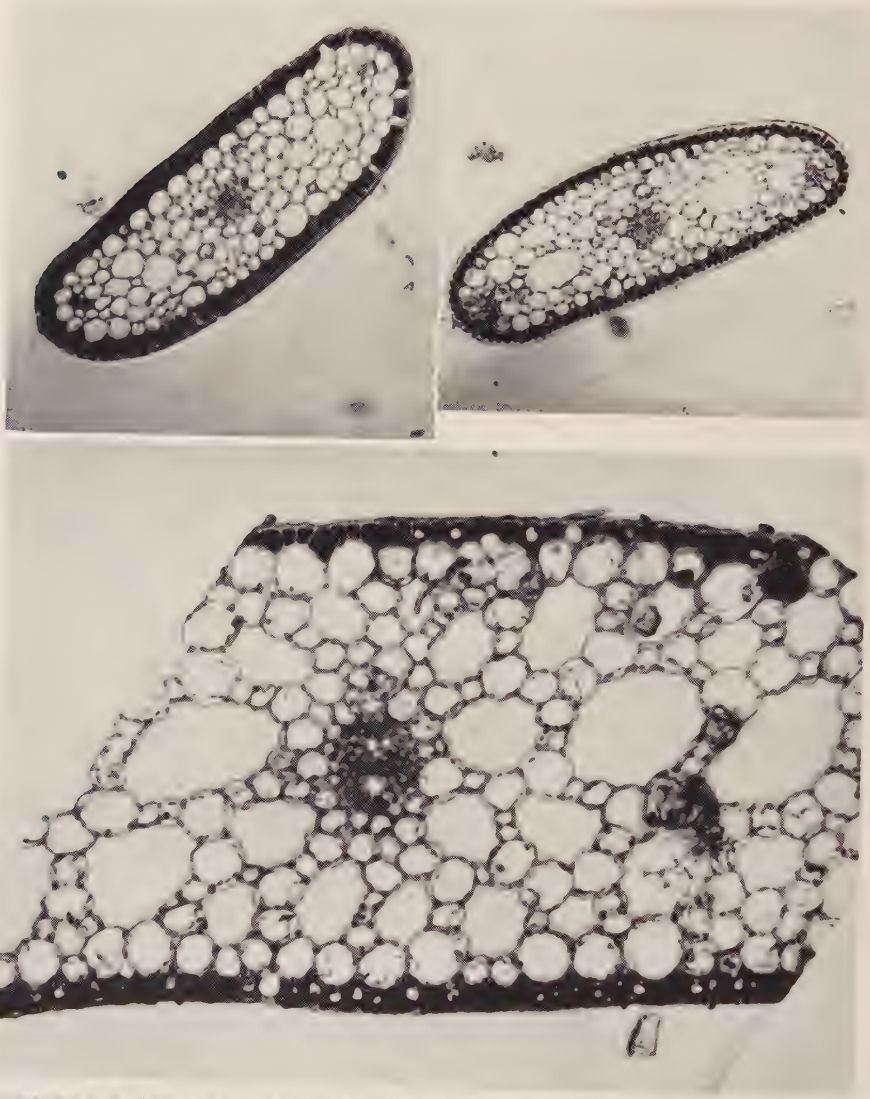
Measurements were made of plants taken from these three zones on Cats Point Bank in Boca Ciega Bay, Pinellas County, on 19 September 1958. It was discovered that not only leaf length but also rhizome thickness and rhizome internode length varied according to the tidal zone in which the plants were found. The plants growing in the zone experiencing exposure on both neap and spring low tides displayed the shortest and narrowest leaves, most narrow rhizomes, and shortest internodes. All increased in size as the tidal zone changed to one of less air exposure. These measurements were: Plants exposed at all low tides: mature leaves—48-58 mm long, mature leaves—½-⅜ mm wide, rhizome thickness—⅞ mm, internode length—0.4-1.2 cm—variable.

Plants only exposed at spring low tides: mature leaves—128-148 mm long, mature leaves—1 mm wide, rhizome thickness—1.5 mm, internode length—0.3-0.5 cm—constant.

Plants never exposed: mature leaves — 134-362 mm long, mature leaves — 1.5 mm wide, rhizome thickness — 1 1/3 mm, internode length—1-2 cm—variable.

These measurements are applicable to plants occurring in these zones in all areas observed.

An investigation was made of the leaf cellular and apical form structure of plants in the three tidal zones. A cross-section of the basal



FIGURES 6-8. X-section of *D. wrightii* leaves at base, just above the ensheathing portions. Fig. 6. From zone exposed to air at all low tides, Longboat Key, Sarasota Bay, October 23, 1958. Note compactness of cells around midvein. 400X. Fig. 7. From zone only exposed to air on spring low tides, Longboat Key, Sarasota Bay, October 23, 1958. Note lacunae becoming evident. Seemingly an intermediate condition between leaves in Figs. 4-5 and Fig. 8. 290X. Fig. 8. From zone never exposed at any low tides, Tarpon Springs, September 30, 1958. Note large conspicuous lacunae surrounding midvein. 255X.

portion of leaves occurring in the zone which is exposed at all low tides is shown in Figure 6. This is almost identical to the structure of leaves of *D. uninervis*. From a cross-section of leaves from the zone exposed only at the spring low tide it is seen the lacunae around the midvein are slightly more evident, a condition clearly intermediate between the leaves from the first and third zone (Fig. 7). The structure of the basal portion of leaves from the zone never exposed is typical of that given by Sauvageau *(op. cit.)* for *D. wrightii* (Fig. 8).

Occasionally variation in this sequence is observed. On 19 September 1958 at Cats Point Bank leaves collected from the zone exposed at all low tides and the zone never exposed displayed the compact arrangement around the midvein which is typical of *D. uninervis*. The structure of the leaves from the zone exposed only at the spring slack low tides at this station was conspicuously typical for that described for *D. wrightii*. The tissue around the midvein of leaves from one station in Tampa Bay in an area exposed at all low tides was so compact that no intercellular spaces were present around the midvein (Fig. 4).

In considering the form of the leaf apex it is concluded that the number of projections is highly variable. Only mature leaves were studied. Plants collected in the zone exposed at all low tides were seen both with and without three points at the leaf apex. Leaves from this zone at Tarpon Springs on 30 September 1958 were found with three points at the apex and with no lacunae around the midvein. This was also seen on plants collected from Longboat Key in Sarasota Bay, 23 October 1958. Both these factors are typical of *D. uninervis*. Leaves collected from this zone at Clearwater Beach on 13 November 1957 were observed to have only two marginal points at the leaf apex, and no conspicuous lacunae were present around the midvein.

In leaves occurring in the zone exposed only at the spring low tide, collected from Longboat Key in Sarasota Bay on 23 October 1958, three points were seen on the leaf apices, and lacunae were just beginning to become evident. These leaves, therefore, incorporate one characteristic of each species.

Leaves collected at Tarpon Springs on 30 September 1958 from an area never exposed presented only two points at the apex, and had large conspicuous lacunae around the midvein. These characteristics are typical of *D. wrightii*.

Isotype material of *D. wrightii* was lent for study by the New York

Botanical Garden through the kindness of Dr. B. Maguire, Curator and Coordinator of Tropical Research. This material was collected by C. Wright from Cuba in 1862. The name on the herbarium label was *Halodule? wrightii* Asch. No leaf sectioning was done on this isotypic material. Two of the growth forms, described above, were present on the sheet, probably representing collection from two tidal zones. The first consisted of dwarf-sized plants, which, if the previous observations may be applied here, were collected in an area exposed at all low tides. The leaf lengths and widths were almost exactly those of dwarf-sized plants previously measured from stations in Florida. Most of the mature leaves in this size class had only two marginal projections present at the leaf apex which is typical of *D. wrightii;* however, occasionally mature leaves were found with three projections.

The other size classification in the isotypic material was the intermediate size probably found in the zone exposed only at spring low tides. Leaf lengths and widths also closely approximated those recorded from Florida stations in the same zone. Because most of the leaves in this size class did not have the original apex present, no remarks may be made concerning the number of projections at the apex. Several of the younger leaves had the original tip present; however, these would tend to be more variable on this aspect, according to the earlier observations of Sauvageau *(op. cit.).*

It is concluded that the habitat affects the growth of *Diplanthera.* According to my observations the two characters given by Sauvageau *(op. cit.)* are not adequate for distinguishing sterile specimens of *D. uninervis* and *D. wrightii.*

Ascherson and Graebner (1907) listed only one character which could be used for comparing differences in the flowers of the two species. The anthers of *D. uninervis* were recorded as being three millimeters long, while those of *D. wrightii* were six millimeters long. If anther length varies with the habitat as has been shown here for leaf and rhizome internode length, it is possible that *D. uninervis* and *D. wrightii* are the same species. However, until a detailed study is made of the inflorescences of the two species and a tidal zone study of *D. uninervis,* the question of the status of these two species names cannot be settled.

ACKNOWLEDGMENTS

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TURBULENT DIFFUSION IN THE SEA[1]

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ABSTRACT

The diffusion equations of Goldstein-Michelson and Joseph-Sendner are examined in the light of experimental evidence derived from a Stommel-Richardson-type experiment. It is concluded that the Goldstein-Michelson theory is approximately valid for the small-scale experiment performed, but that modifications may be necessary for a proper description of diffusion from an initially very small to a terminally very large scale. The velocity autocorrelation function implicit in the Goldstein-Michelson theory, if appropriately modified, could be incorporated into a diffusion equation which would describe the empirical increase in diffusivity with increasing scale.

INTRODUCTION

In oceanography it has generally been assumed that turbulent diffusion is adequately described by the classical diffusion equation:

$$\frac{\partial c}{\partial t} = D \nabla^2 c \qquad (1)$$

in which c is the concentration of diffusate and D is the turbulent, or eddy, diffusivity. There are, unfortunately, two well-known objections to this equation. The first objection is that it fails to describe the fact that a diffusate "patch" has an outer border which progresses outward with a finite speed, i.e., the equation gives a description in which endless "tails" are extended instantaneously from the initial distribution. The second objection is that this equation has a single value for the eddy diffusivity, although it has been noted repeatedly that the phenomenological diffusivity, defined (in 2 dimensions) by

$$D^* = \frac{1}{4} \frac{d}{dt} \langle r^2 \rangle$$

is larger in proportion to the geometric scale of the experiment or measurement by which it is determined (Stommel, 1949 or Joseph and Sendner, 1958). Modified diffusion equations have been proposed to answer these objections, and two of them will be discussed here briefly.

A quantitative understanding of turbulent diffusion in the sea is useful for two reasons: it enables us to evaluate and to predict various natural mixing processes and the distributions of salinity, temperature, radioactive waste, etc. resulting from them; it provides an indirect source of information about the statistical properties of turbulent

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motion. The connection between turbulence and diffusion is indicated by the relation (Kampé de Fériet, 1939) between the mean-square dispersion of diffusate, released at the coordinate origin, and the turbulent velocity correlation function $R(t)$:

$$\langle r^2 \rangle = 2 \int_0^t (t - t') R(t') \, dt' \qquad (2)$$

or alternatively

$$\frac{d^2}{dt^2} \langle r^2 \rangle = 2 R(t) \qquad (2a)$$

The velocity correlation function is defined by

$$R(t) = \langle v(t') \cdot v(t'+t) \rangle \qquad (3)$$

where the brackets indicate a suitable average over the turbulent velocity fluctuations v. These velocity correlations are the chief object of study in the theory of turbulent motion (see, e.g., Batchelor, 1956).

Experimental Procedure

The results of a preliminary experiment carried out at The Marine Laboratory of the University of Miami and its bearing on the various theories of turbulent diffusion discussed will be reviewed.

The experiment was conducted in a region in the Atlantic Ocean east of Elliott Key in water about 15 feet deep. The wind was from the northeast at an estimated 15 miles per hour.

Four groups of floats were placed in the water, each group being about one-half mile from its neighbor. Group A consisted of 11 floats; groups B, C, and D contained 10 floats each. For size reference a wooden board 4 feet long, painted white, was placed in the water adjacent to each group. The floats were sheets of standard mimeograph paper, which provide excellent visibility and which float just under, or at, the surface of the water thus being relatively unaffected by the wind.

The groups of floats were then photographed at timed intervals of approximately 16 minutes; the photographs were taken from a seaplane flying at an altitude of 500 feet.

It should be noted for the benefit of future investigators that those photographs taken after about an hour and a half were not usable because some of the floats in the group could no longer be located in the exposures. Evidently, therefore, the photographs should be taken from a higher altitude and precautions should be taken to preclude possible saturation and sinking of the paper floats. Another contretemps was

that four groups of floats which had been placed in Biscayne Bay before the ocean groups were distributed, could not be located two hours later, even though the reference boards which accompanied them were readily found.

Unfortunately, group D of the ocean groups was rendered useless because of malfunction of photographic equipment.

Using an arbitrarily placed coordinate system, the centroid (center of mass) of the floats was located on each photograph of the three groups (A, B, and C). The distance r from the centroid was then computed for each float. These values are listed in Tables 1, 2, 3.

TABLE 1
DISTANCE OF FLOATS FROM CENTROID IN METERS
GROUP A

Photo 1	Photo 2	Photo 3	Photo 4	Photo 5
12.38	11.17	14.41	22.13	22.94
4.26	5.68	8.93	17.26	22.13
3.25	3.65	9.14	16.85	17.46
3.65	3.25	6.50	10.96	12.59
2.64	3.05	3.25	1.83	10.76
3.25	1.83	6.50	2.44	5.89
1.83	6.29	0.61	6.29	3.86
6.29	2.44	5.68	7.92	16.24
6.09	6.50	10.56	11.37	23.14
5.89	6.50	11.37	16.04	23.14
6.09	10.96	14.21	22.33	28.42
$\langle r \rangle$ = 5.06	5.57	8.29	12.31	16.96

Time interval between photos:

1 and 2
2 and 3
3 and 4
} 16 min.

4 and 5 — 15 min.
Total time: 63 min. (3780 sec.)

THE GOLDSTEIN-MICHELSON EQUATION

A hyperbolic (i.e., wave-type) diffusion equation (Goldstein, 1951) which was later extended (Michelson, 1954) has its foundation in a stochastic analysis of the random-walk in which a tendency for flights to persist in their direction is taken into account. It has the form

$$\frac{\partial c}{\partial t} = D \nabla^2 c - \frac{D}{v^2} \frac{\partial^2 c}{\partial t^2} \qquad (4)$$

TABLE 2
DISTANCE OF FLOATS FROM CENTROID IN METERS
GROUP B

	Photo 1	Photo 2	Photo 3	Photo 4	Photo 5
	12.18	19.29	18.68	32.07	28.22
	3.65	8.73	15.63	21.52	27.61
	4.67	9.14	17.26	19.08	13.60
	2.23	10.15	6.70	11.77	18.27
	2.44	6.50	7.71	16.04	2.03
	7.11	7.92	2.84	1.22	10.76
	3.45	9.95	18.86	9.54	15.23
	4.47	7.11	18.07	17.86	19.89
	5.28	13.80	17.26	24.16	27.81
	5.08	13.20	26.39	24.36	32.68
$\langle r \rangle$ =	5.06	10.58	14.92	17.76	19.61

Time — same as Table 1.

TABLE 3
DISTANCE OF FLOATS FROM CENTROID IN METERS
GROUP C

	Photo 1	Photo 2	Photo 3	Photo 4	Photo 5
	7.92	18.68	26.59	24.97	27.61
	6.50	17.66	24.56	22.33	27.81
	2.84	11.57	14.41	17.05	17.66
	0.20	8.32	9.34	13.20	16.44
	2.44	2.23	8.93	6.50	7.71
	1.62	5.68	2.23	10.96	15.63
	2.03	10.96	12.99	10.96	15.43
	2.64	11.57	17.46	18.88	20.71
	3.65	16.44	28.22	24.56	25.38
	5.48	18.88	29.84	31.26	33.70
$\langle r \rangle$ =	3.53	12.20	17.46	18.07	20.81

Time — same as Table 1.

This reduces to the classical equation when the random flight velocity v increases without limit. The solutions of this equation describe damped waves. The objection to the classical equation, that it did not represent diffusion with finite speed, is thus answered since the damped waves propagate with finite speed.

In equation 4) since $c \geq 0$, where $c = c(x, t)$, and since c can be normalized to unity, i.e., $\int c(x,t)dx = Q = 1$, c may be considered a probability density function, and $\int x^2 c\, dx = \langle x^2 \rangle$. Multiplying Eq. 4) by x^2 and integrating with respect to x from $-\infty$ to ∞ gives, after two partial integrations,

$$\frac{d}{dt}\langle x^2\rangle = 2D - \frac{D}{v^2}\frac{d^2}{dt^2}\langle x^2\rangle$$

assuming that $xc \longrightarrow o$ and

$$x^2 \frac{\partial c}{\partial x} \longrightarrow o \quad \text{as} \quad |x| \longrightarrow \infty$$

Similarly, from the one-dimensional equation for diffusion along the Y-axis

$$\frac{d}{dt}\langle y^2\rangle = 2D - \frac{D}{v^2}\frac{d^2}{dt^2}\langle y^2\rangle$$

since the process in the y direction is identical to that in the x direction and is independent of it.

Adding these last two equations gives

$$\frac{d}{dt}\langle r^2\rangle = 4D - \frac{D}{v^2}\frac{d^2}{dt^2}\langle r^2\rangle \qquad (5)$$

A solution of Eq. 5) is

$$\langle r^2\rangle = 4Dt + \langle r^2\rangle_o \qquad (6)$$

It satisfies the boundary conditions

$$\langle r^2\rangle = \langle r^2\rangle_o$$

$$\frac{d}{dt}\langle r^2\rangle = 4D \quad \text{at} \quad t = o,$$

and agrees with the classical diffusion equation solution.

Another solution of Eq. 5) is

$$\langle r^2\rangle = 4Dt + 4D\tau\,(e^{-t/\tau} - 1) \qquad (7)$$

which satisfies, at t = O, boundary conditions

$$\frac{d}{dt}\langle r^2\rangle = O \quad \text{and} \quad \langle r^2\rangle = O.$$

These initial conditions were not realized in the experiment described here; they imply a point source and an initial diffusion rate of zero. They are, however, the boundary conditions implicit in the Kampé de Fériet relation (See Eq. 2a):

$$\frac{d^2}{dt^2}\langle r^2\rangle = 2R(t)$$

Differentiating Eq. 7) twice gives

$$\frac{d^2}{dt^2}\langle r^2\rangle = \frac{4D}{\tau} e^{-t/\tau} \tag{8}$$

Comparing Eq. 8) with Eq. 2a), it can be seen that they agree if

$$R(t) = \frac{2D}{\tau} e^{-t/\tau} = \langle v^2\rangle e^{-t/\tau} \tag{9}$$

since $\langle v^2{}_1\rangle = \langle v^2{}_2\rangle$.

The parameters v^2 and τ of the autocorrelation function $R = v^2 e^{-t/\tau}$ can be explicitly evaluated from the experimental data. The graph of $\langle r^2\rangle$ versus time (Fig. 1) which was plotted from the values in Table 4 gives a straight line from which, by the use of Eq. 6), D is determined to be

$$D = 270 \text{ cm}^2/\text{sec.} \tag{10}$$

This somewhat small value is due to the fact that the experiment was performed in shallow water (15 feet deep). It should be explained here that the velocity v in the autocorrelation function is approximately the velocity of the outer edge of the diffusate, or, in our case, the rate at which the radius represented by the largest r (See Tables 1, 2, 3) of the "patch" in each photograph increases. v was found to be

$$V = .54 \text{ cm./sec.} \tag{11}$$

Combining the value for v with the value for D mentioned above yields

$$\tau = \frac{D}{v^2} = 930 \text{ secs.} \tag{12}$$

This is the time scale of correlation and is a measure of approximately how long, on the average, a turbulent fluid motion persists before changing direction or speed. The travel distance associated with it is

$$L = v\tau \simeq 5 \text{ meters} \tag{13}$$

This value may be regarded as a sort of mixing length because 12) and 13) imply the "classical" relation $D = vL$ (Sverdrup, Johnson, and Fleming, 1942). It is noteworthy that the mixing length of 5 meters agrees remarkably well with the water depth, i.e., about 4.5 meters. Water of this depth, especially with irregular bottom topography as in the experimental site, can be assumed to be unstratified and to approximate isotropic turbulence in its motion. On account

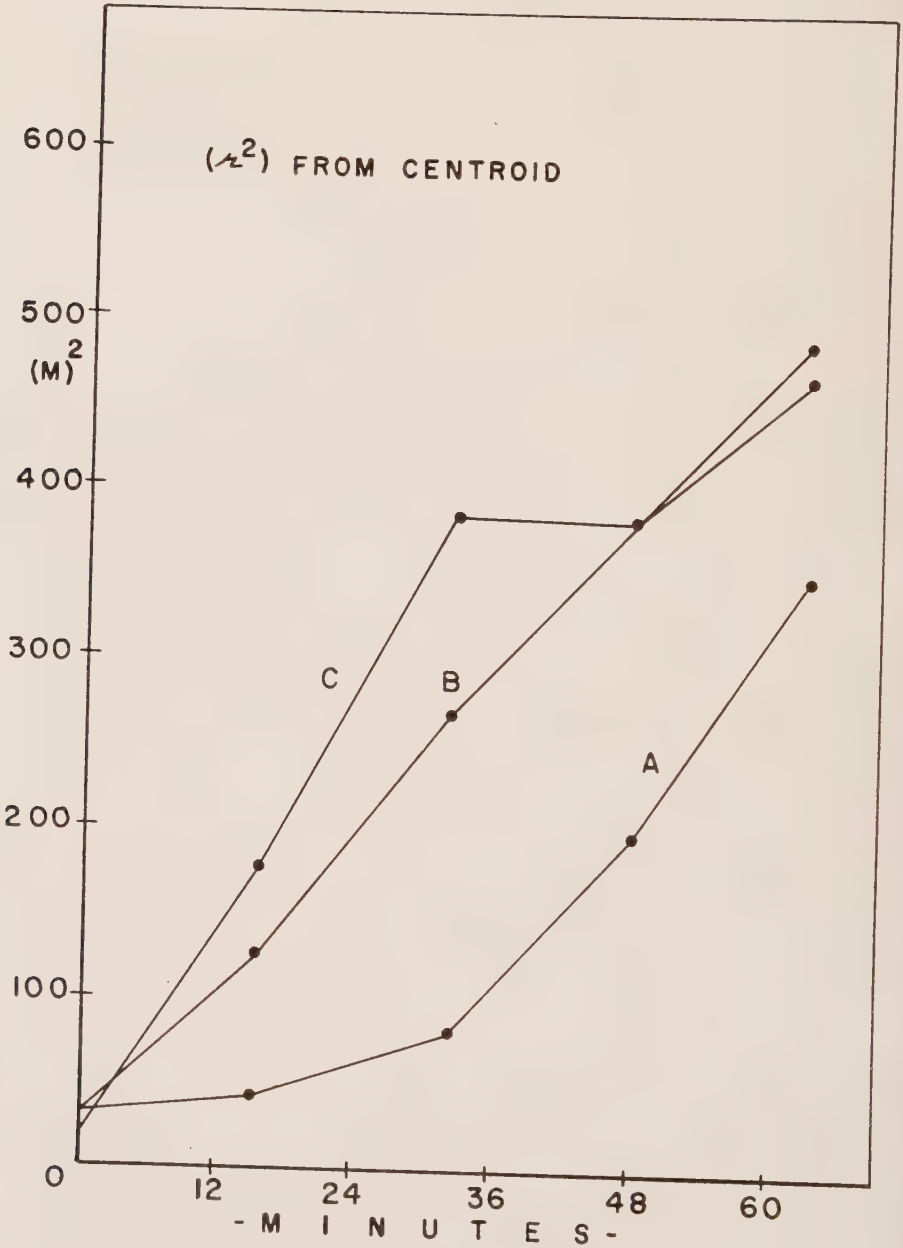

FIGURE 1. $<r^2>$ from centroid.

of this isotropicity it is not surprising that the horizontal space-scale of turbulence should be of the same order of size as the water depth.

The Equation of Joseph and Sendner

Recently a modification of the classical diffusion equation has been proposed (Joseph and Sendner, 1958) for application in oceanography. [An alternative derivation has been given (Bourret, 1959).] It may be written (in two dimensions) as

$$\frac{\partial c}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left(\frac{v}{2} r^2 \frac{\partial c}{\partial r}\right) \tag{14}$$

This expression does not correspond to diffusion with finite turbulent velocities, although the concentration of diffusate falls off rapidly when $r > vt$. By multiplying this equation by r^2 and forming averages over the surface area the following relation is obtained:

$$\frac{d}{dt}\langle r^2 \rangle = 3\, v \langle r \rangle \tag{15}$$

Multiplying 14) by r and forming the space average gives

$$\frac{d}{dt}\langle r \rangle = v \tag{16}$$

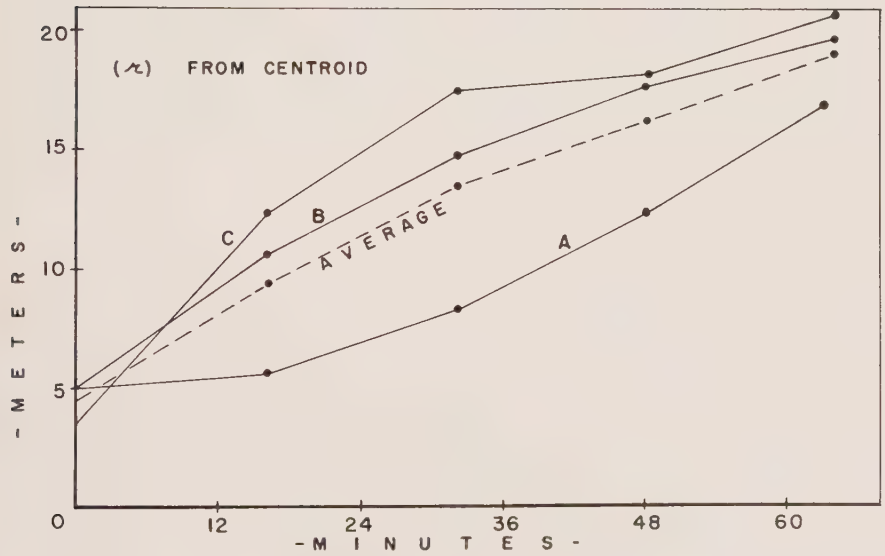

Figure 2. $\langle r \rangle$ from centroid.

Combining these results and integrating yields

$$\langle r^2 \rangle = \frac{3}{2} v^2 t^2 + 3v \langle r \rangle_o \, t + \langle r^2 \rangle_o \qquad (17)$$

The experimental data yield the values for the constants:

$$\langle r^2 \rangle_o = 2.8 \times 10^5 \text{ cm}^2 \qquad \text{(Table 4)}$$
$$\langle r \rangle_o = 4.6 \times 10^2 \text{ cm} \qquad \text{(Tables 1, 2, 3)} \qquad (18)$$
$$v = \frac{d}{dt} \langle r \rangle = .4 \text{ cm/sec} \qquad \text{(Tables 1, 2, 3)}$$

Using these values, 17) has been plotted in Fig. 4). This parabolic curve provides a satisfactory description of the data only for the early portion of the experiment. Towards the end it begins to diverge from

FIGURE 3. Photograph of group of floats.

TABLE 4

$\langle$(DISTANCE)$^2\rangle$ FROM CENTROID OF FLOATS IN EACH GROUP $\langle$(IN (METERS)$^2\rangle$

Photo No.	Group A	Group B	Group C	$\langle r^2 \rangle$
1	33.25	33.34	17.63	28.07
2	40.66	125.87	179.26	115.26
3	83.02	267.39	385.06	245.16
4	199.37	384.48	381.55	321.80
5	350.00	466.10	486.98	434.33

$$\langle \text{Dist.}^2 \rangle = \langle r^2 \rangle = \frac{1}{N} \sum_{i=1}^{N} (\langle x_i^2 \rangle + \langle y_i^2 \rangle)$$

Number of floats N = 11 for group A
N = 10 for B, C, D.

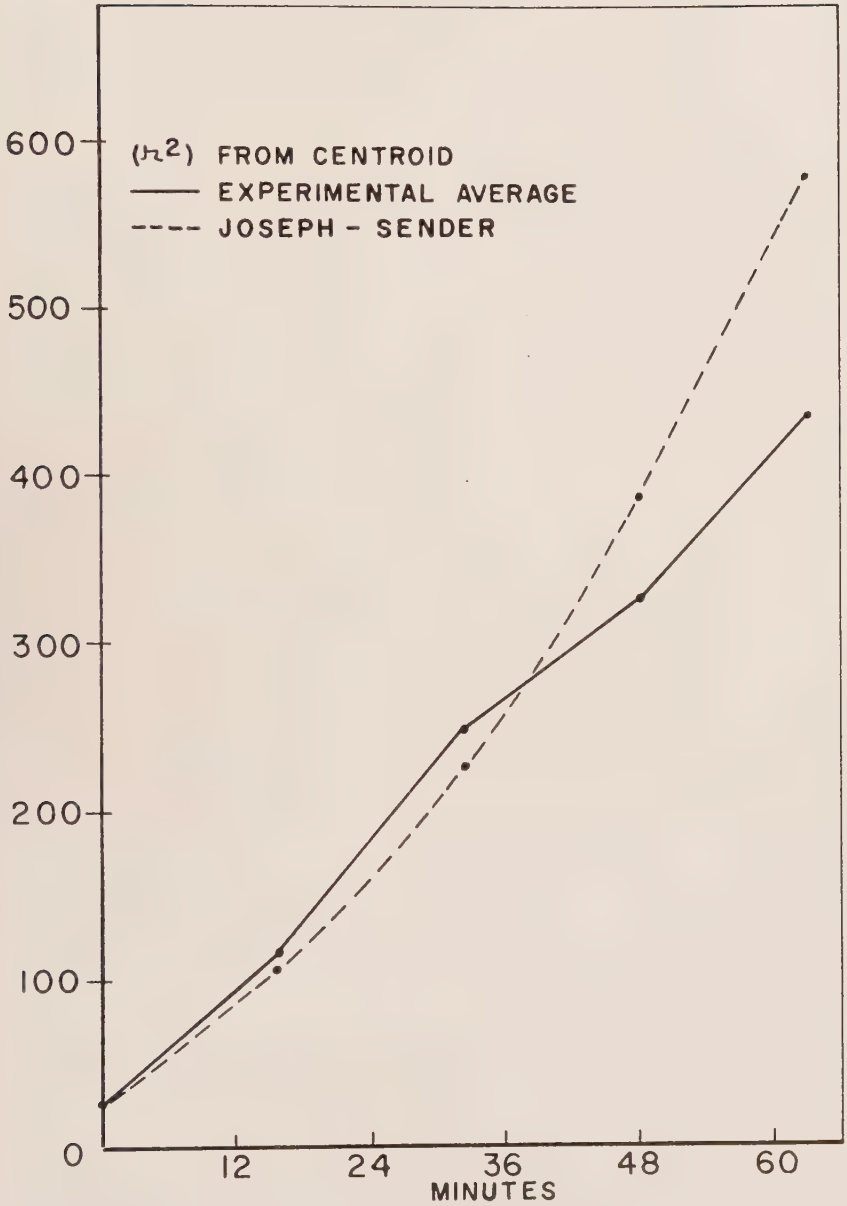

FIGURE 4. $<r^2>$ from centroid.

the observed values, and presumably would do so more markedly if the experiment were protracted further.

Discussion

From the preliminary experiment described the approximate validity of the Goldstein-Michelson theory of diffusion has been demonstrated. No strong conclusions can be reached concerning the adequacy of the Joseph-Sendner formulation. It can only be said that it does not markedly contradict the facts, although it does appear somewhat less satisfactory than the Goldstein-Michelson description for the small scale experiment performed. Since the increase in appearent, or phenomenological, diffusivity with experimental scale is fairly well established it may be expected that the Goldstein-Michelson equation will also prove inadequate to the description of diffusion over a wide range in size, i.e., from initially very small to terminally very large scale. When this happens, either the Goldstein-Michelson equation must be revised in some way in order to take this into account, or the Joseph-Sendner (or some similar) equation must be utilized. Because the latter appears to have a rather arbitrary basis, it is preferable to consider a physically meaningful modification of the Goldstein-Michelson equation. At the present time, only an outline of how this might be accomplished can be given.

To begin with, we consider the putative explanation of the appearent increase in diffusivity with experimental scale: that as the diffusate patch increases in size, larger and larger eddies are brought into play as diffusive agents. As long as an increase in scale brings about the inclusions of larger eddies, i.e., as long as there is organized or coherent flow of a size or scale larger than the region occupied by the experimental diffusate patch, there will be a progressive increase of appearant diffusivity with time—and, therefore, with scale. Since classically

$$<r^2> = 4Dt + <r^2>_0 \qquad (19)$$

in two dimensions, the "phenomenological" diffusivity may be defined by

$$D^* = \frac{1}{4}\frac{d}{dt}<r^2> = \frac{1}{2}\int_0^t R\,(t')dt' \qquad (20)$$

the second equality holding by virtue of Equation 2a). If D^* is to increase monotonically with t, then R must be chosen so as to make this possible. This seems a reasonable procedure because it implies,

in terms of turbulent velocity fluctuations, that there exist correlated motions over larger and larger times. In a previous work (Bourret, 1959a) it has been shown that the (one-dimensional) velocity autocorrelation function implicit in the Goldstein-Michelson equation is the exponential

$$<v^2> e^{-t/\tau} \qquad (21)$$

This is essentially due to the assumption that the velocity fluctuations constitute a Markov process (see e.g., Wang and Uhlenbeck, 1945). If this were modified so that the integral of R(t) were a monotone increasing function of t in accordance with Equation 20) the desired description of the growth of $<r^2>$ in a physically acceptable way would be achieved.

The above would not, however, give a complete description of the process of diffusion. Higher moments of the distribution, for example, would still be unknown. For this complete description a diffusion *equation* is needed, and in order to incorporate the scale dependence described it should involve the function R. Such an equation has been recently proposed by Bourret in the work last cited (Bourret, 1959a). It takes the form (for two-dimensional isotropic turbulence)

$$\frac{\partial c}{\partial t} = \sum_{k=1}^{2} \frac{\partial^2}{\partial x_k^2} \int_0^t R_{kk}(t') C(x, y, t-t') \, dt' \qquad (22)$$

where

$$R_{kk}(t') = <v_k(t) \, v_k(t+t')>$$

The results of the preliminary experiment provide evidence that further investigations of two-dimensional diffusion processes in the ocean are indicated. By increasing the number of observed groups of diffusing floats and by increasing the total number of floats in each group, better statistical averages can be obtained. Also, the time interval between successive measurements of each group, if somewhat shortened, will lead to a better quantitative understanding of the phenomena involved.

The foregoing modifications in the experimental procedure should, if the total time of observation is at least doubled, provide valuable data for determining the shape of such curves so that better comparison can be made with the theoretical conclusions of Kampé de Fériet, Goldstein-Michelson, and Joseph-Sendner.

An experiment should also be conducted in an area where the bottom has a known gradual slope. This variation of water depth will

allow for more accurate determination of the possible relation between water depth and mixing length which was discussed earlier.

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The degree of comprehensiveness of the bibliography is to a large extent dependent upon the cooperation of workers in the Marine Sciences of this area. *It is therefore hoped that individuals and organizations will aid by sending copies of all relevant publications to the Editor.* Any omissions brought to the attention of the Editor will be included in subsequent issues.

It has been found convenient to use a modification of the classification used by the Journal du Conseil Bibliography for present purposes.

The Editorial staff wishes to acknowledge the valuable assistance given by a number of investigators in compiling the bibliography.

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